JOURNAL OF THE

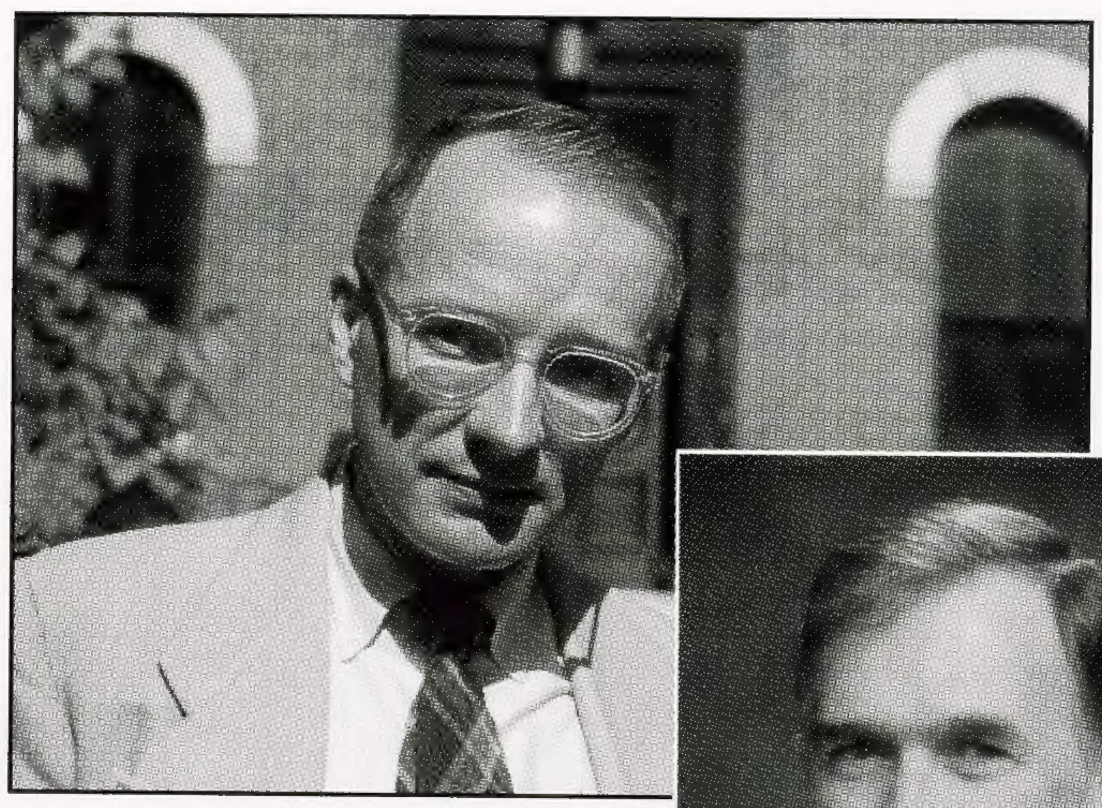
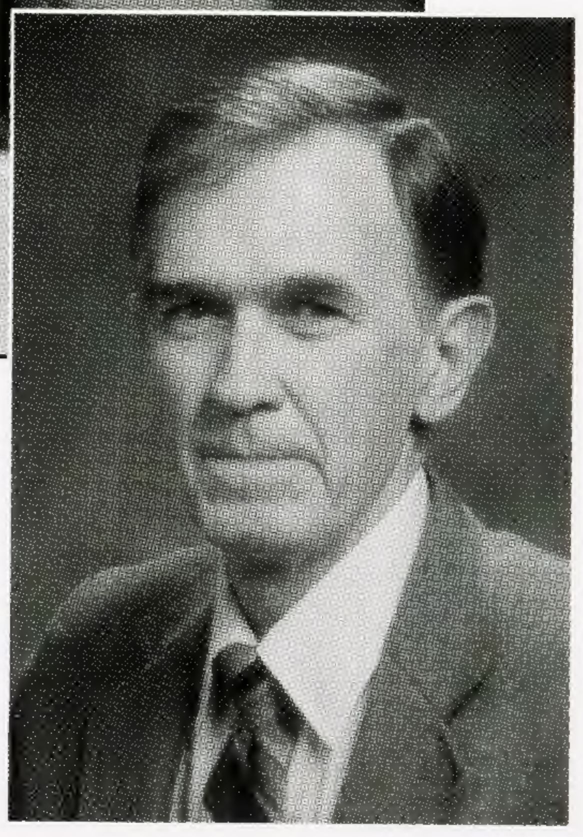
BOTANICAL RESEARCH INSTITUTE OF TEXAS

VOLUME 3, NUMBER 1, 15 JULY 2009

Journal of the Botanical Research Institute of Texas

J. Bot. Res. Inst. Texas ISSN 1934-5259

VOLUME 3 **NUMBER 1** **15 JULY 2009**

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Bibliographical

Citation abbreviation for the *Journal of the Botanical Research Institute of Texas* is *J. Bot. Res. Inst. Texas* following the principles of B.P.H. (informally *JBRIT*). International Standard Serial No. (ISSN 1934-5259)

Frequency of Publication

J. Bot. Res. Inst. Texas is published semiannually (summer/fall) as one volume by the Botanical Research Institute of Texas.

Copyright 2009
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Fort Worth, Texas 76102-4025, USA

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Subscription Prices (2009)

$43. Personal (Individual/Family)
$95. USA (Institutional)
$105. Outside USA (Institutional)

Subscriptions/Back Volumes

J. Bot. Res. Inst. Texas and *Sida, Contr. Bot.*
Publications Assistant
Botanical Research Institute of Texas
500 East 4th Street
Fort Worth, Texas 76102-4025, USA
Electronic mail: orders@brit.org

Composition

rhorngraphics, Plano, Texas; rlrchorn@verizon.net

Printing

Prepress production and printing in the United States of America by Millet the Printer, Dallas, Texas
www.millettheprinter.com

Cover Illustration

Electronically tinted botanical illustration of *Liatris aestivalis* originally used on BRIT's anniversary poster 2001. Summer gayfeather flowers mid Jul–Aug(–Sep) and is endemic to Oklahoma and Texas. Sida 19:768. 2001. Botanical illustration by Linny Heagy ©2001.

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COMMENTARY

LEARNING ABOUT OTHER SPECIES: AN UPDATED COMPONENT OF A LIBERAL ARTS EDUCATION

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Some aspects of a liberal arts education—critical thinking, respect for truth and clarity of expression—are unchanging in value. Knowledge of humans and human culture remains central. But if the goal of the curriculum is to prepare students for broad engagement in the world, an understanding of the Earth and all of life calls for equal time.

Humanity is, for now at least, bound to Earth. Here, unbridled growth of the human population and profligate use of natural resources threaten our own existence and put at risk the well-being and continuance of all life and the environment. An appreciation of the planet and preparation toward committed stewardship should be among the primary goals of education. Liberal arts education can not afford to be self-centered, in the sense of study of human culture outside its environmental context and without attention to the thousands of species that are our evolutionary associates.

We propose a course that guides students towards an appreciation of the Earth as home to many species. At the end of the essay, the course is integrated within an updated liberal arts curriculum.

Learn to know other species. Perhaps the most effective path toward an appreciation of life on Earth is through first-hand knowledge of species other than our own. The primary goal of the proposed course is to learn the identities of commonly encountered species. The course need not be heavily laden with deep academic underpinning—the value lies in learning to recognize species by sight, as they are encountered in everyday life, and to identify them by name.

A know-the-species course provides foundation for one of the most basic lessons in humility—humans are one species among hundreds of thousands. So many of us are hardly aware that others exist, except in an abstract way. Daily acquaintance with other species on a "first-name" basis greatly broadens one's view of the natural world and engenders a closeness, a sense of unity, with it. Even if names of species eventually are forgotten, at least the memory remains that each is unique, distinguished by features that most have previously been unaware of.

One can quickly learn to identify a half-dozen species (hollies, oaks, maples, etc.) and to see that some of the species are more similar among themselves while others are more unique. Such an appreciation of variation and diversity, even in a simple system, is the quickest way possible toward real insight into the process of evolution—patterns of similarity among species result from common ancestry. Each species on Earth is the product of long evolutionary lineage, interrelated among the others, each unique and beautiful.

> "I am strongly induced to believe that, as in music, the person who understands every note will, if he also possesses a proper taste, more thoroughly enjoy the whole, so he who examines each part of a fine view, may also thoroughly comprehend the full and combined effect. Hence, a traveller should be a botanist, for in all views plants form the chief embellishment."—**Charles Darwin**, 1836, *Voyage of the Beagle*.

Nature of the course. Plants are the most conspicuous and abundant expression of non-human life, even in urban settings, and we believe they are the best focus for the proposed course. It's joyful to walk along a

sidewalk, through a park, or through the woods and recognize species of oaks, elms, and maples by name. Even in a cityscape, dozens of species are commonly planted and usually many more are scrabbling out their existence, unassisted, seeding themselves in unlikely places.

Awareness of other species also could be gained from an introduction to birds, beetles, fish, or fungi, or practically any other kind of organism, but none of these is as easily accessible as plants. Do other courses in biology (e.g., physiology, genetics, molecular biology, cell biology) offer the same potential insights? Simply, no—most are based on study of a single species or of no species in particular. Some courses in ecology require a basic knowledge of species diversity, but the focus is different. Studies of geology, meteorology, and astronomy may be doorways to recognition of the diversity of everyday extra-human experience and could be analogous to identification of plants, but diversity, or at least every-day accessibility, is much lower.

Residents of the United States and other highly urbanized areas are so removed from other species that it is easy to be unaware that plants underpin our existence. Do undergraduates recognize that our diet is mostly of roots, stems, leaves, fruits, and seeds? Do typical students know that most of the energy expended by human individuals comes directly from starch in corn, rice, cassava, wheat, and potatoes? Beans, bananas, and sorghum are the world's dietary staples. Chocolate, coffee, sugar—the plant foods that tempt us. Cotton, flax, hemp, mulberry—the plants of fashion. Even the meat in our diet is but one step away from plant nutrition. Plants are responsible for nearly all our oxygen, our clothes (directly or indirectly), and most of our non-food energy (fossil fuels ––oil, natural gas, coal). These topics deserve a place in a liberal arts education.

Since the suggested course is not an abstruse undertaking, basic knowledge of other species should be taught not only as part of a liberal arts collegiate education but in elementary through high school as well. Of course, this is one among many basic topics, but lack of knowledgeable teachers is a constraint and the responsibility usually comes to rest at college level.

Suggested course outline. (**A**) identification of 100 species, concentrating on first-hand recognition of those most easily at hand and abundant; (**B**) a brief overview of plant vegetative features and reproduction (flower and fruit structure usually are critical in identification) and common families encountered among the species; (**C**) perspectives on evolution, the interrelatedness of life, and global patterns of diversity; and (**D**) a brief introduction to ecological and economic values of plants encountered in everyday life (e.g., urban forests, invasive species, food, clothes, construction, fuel). Simply learning to know the species is the first priority.

Goals of a liberal arts education. In the broad view, we believe that a liberal arts curriculum should be aimed (**1**) toward continued existence of our own species and all others and (**2**) toward maximizing the potential for freedom and happiness (including creativity, appreciation of beauty, productivity, service, and increasing understanding of the world).

Overview of an updated liberal arts curriculum. We divide a suggested curriculum into four major, overlapping categories.

1. ***The Earth and all things non-human.*** Life and life processes (humans as animals, other species, ecology, evolution), geology, weather and climatology. Our proposed course would figure as a central focus in this category.
2. ***Intellectual outlook.*** Reasoning and critical thinking (including scientific method), respect for truth, clarity of expression, philosophy and ethics.
3. ***Humans and human culture.*** Beauty (visual art, music, perception), cultural diversity and history (history, language, philosophy, ethics, and religion).
4. ***The Universe and universal principles.*** Astronomy and cosmology, physics and chemistry, mathematics.

OROBANCHE RIPARIA (OROBANCHACEAE), A NEW SPECIES FROM THE AMERICAN MIDWEST

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ABSTRACT

Orobanche ludoviciana, with a range primarily in the Great Plains, is the most widely distributed species in sect. *Nothaphyllon*. It was first described by Thomas Nuttall in 1818 from a specimen collected at Ft. Mandan, North Dakota. During the following century and a half, most botanists had limited field experience with living plants of the genus and very few herbarium specimens with which to compare newly collected materials. This resulted in considerable confusion about the circumscription of this species and its geographic distribution. The treatments of Section *Nothaphyllon* (sect. *Myzorrhiza*) by Beck (1890, 1930) and Munz (1930) have led botanists to apply the species name too broadly to plants whose morphology was discordant with Nuttall's original protologue, and the problem of an overly broad species concept continues to linger. Earlier studies by the senior author led him to suggest taxonomic changes within the *O. ludoviciana* complex (Collins 1973) to address this problem, including formal recognition of two ecological races within *O. ludoviciana* sensu stricto with different host ranges: one inhabiting uplands and the other confined to bottomlands associated with major river systems. Recent additional investigations have revealed further evidence supporting recognition of these two races as distinct taxonomic entities. The present paper therefore discusses the morphological distinctions between them; it proposes retention of the upland form as *O. ludoviciana* and recognition the bottomland form as a distinct species, **O. riparia,** sp. nov.

RESUMEN

Orobanche ludoviciana, cuya extensión abarca mayormente la zona de Great Plains, es la especie de mayor distribución en la Sección *Nothaphyllon*. El primero que hizo una descripción fue Thomas Nuttall en 1818, que se basó en una muestra recogida en Ft. Mandan, Dakota del Norte. Durante el siglo siguiente la mayoría de los botánicos tenían poca experiencia con plantas vivas de ese género y con ejemplares de herbario con las que comparar los materiales obtenidos. Por consiguiente hubo bastante confusión en torno a la circunscripción de esta especie y su distribución geográfica. Los estudios relacionados con la Sección *Nothaphyllon* (sec. *Myzorrhiza*) hechos por Beck (1890, 1930) y Munz (1930) hacen que los botánicos apliquen de modo demasiado amplio los nombres de las plantas cuya morfología es discordante con el protólogo original de Nuttall. El problema que permanece es el de un concepto demasiado amplio de la especie. Estudios doctorales conducidos por el autor principal durante los primeros años de la década de los setenta resultaron en cierto número de cambios taxonómicos sugeridos en el complejo *O. ludoviciana* (Collins 1973), incluso un reconocimiento formal de dos razas ecológicas dentro de *O. ludoviciana* sensu stricto con distribución algo diferente de los huéspedes. Una de las plantas era de tierras altas y es retenida aquí como *O. ludoviciana* y la otra confinada a tierras bajas asociadas principalmente con sistemas mayores fluviales y reconocida aquí como entidad sin descripción. Recientemente han salido a la luz más datos que apoyan dicha propuesta. En el presente trabajo se comentan las diferencias morfológicas entre estos dos ecotipos y se propone reconocer las poblaciones de las tierras bajas como una especie distinta **O. riparia,** sp. nov.

Key Words: *Orobanche*, Orobanchaceae, parasitic plants, broomrape, Flora of North America

Orobanche L. sect. *Nothaphyllon* (A. Gray) Heckard (sect. *Myzorrhiza* Phil.) comprises of an array of ca. 13 species that account for most of the taxonomic diversity within New World holoparasitic Orobanchaceae. It has been considered a monophyletic group by most botanists based on morphological and molecular data (Olmstead et al. 2001; Schneeweiss et al 2004; Bennett & Matthews 2006). Within sect. *Nothaphyllon*, two

major clades exist whose relationships have not yet been fully resolved: the *O. californica* Cham. & Schltdl. complex (Heckard 1973), which has diversified mainly in the far-western United States; and the *O. ludoviciana* Nutt. complex (Collins 1973), which is widespread in the remainder of the United States and Canada, and southward into Mexico (also disjunct in southern South America).

Orobanche ludoviciana Nutt., with a range primarily in the Great Plains, is the most widely distributed species in sect. *Nothaphyllon*. It was first described by Thomas Nuttall in 1818 from a specimen collected at Ft. Mandan, North Dakota. Because most botanists during the following century had limited field experience with living plants of the genus and had very few herbarium specimens with which to compare newly collected materials, the species name was applied too broadly to include plants whose morphology is discordant with Nuttall's original protologue. The result has been considerable confusion about the circumscription of this species and its geographic distribution. All those who have treated Section *Nothaphyllon* (sect. *Myzorrhiza*) (Beck 1890, 1930; Munz 1930; Collins 1973; Heckard 1973), have at times recognized various infraspecific taxa, some of which are no longer accepted and therefore excluded from this discussion. Nevertheless, the lingering problem has been that of an overly broad species concept. Even Philip Munz (1930), who provided good insights into taxonomic variation within *O. ludoviciana* in his otherwise excellent taxonomic revision of sect. *Myzorrhiza*, overlooked significant morphological variation. Subsequent authors of floristic works who relied on his revision to determine specimens continued to some degree to overlook the taxonomic heterogeneity of plants treated by him as *O. ludoviciana* var. *genuina* Beck.

Doctoral studies by the senior author led him to suggest a number of taxonomic changes within the *O. ludoviciana* complex (Collins 1973), one of which was formal recognition of two ecological races within *O. ludoviciana* sensu stricto with differing host preferences: one inhabiting only uplands and the other confined to bottomlands associated with major river systems. Recent discoveries of new populations and examination of additional existing herbarium specimens of the bottomland plants have added evidence in support of this proposal. The present paper therefore discusses the morphological distinctions between these two ecotypes, and we propose to retain the upland form as *O. ludoviciana* and to recognize the bottomland form as a distinct species, *O. riparia*. It should be noted that, based on Collins's dissertation, the epithet *O. riparia* was discussed far in advance of the present publication by Musselman (1982, on Orobanchaceae in Virginia) and by Kartesz (1994, in a North American plant checklist), but neither of these usages affects the validity of the present description.

Bringing this new taxon to the botanical literature requires a brief review of the existing nomenclature and morphology of *O. ludoviciana* sensu stricto (*O. ludoviciana* var. *genuina*, sensu Beck). Several species of *Orobanche* in North America are commonly misidentified as *O. ludoviciana*, but are currently recognized as distinct species. They include *O. multiflora* Nutt., *O. cooperi* (A. Gray) A. Heller, *O. multicaulis* Brandegee, and *O. valida* Jepson. Of these, the two with the most morphological similarity and name association are *O. ludoviciana* and *O. cooperi*, and must therefore be contrasted with *O. riparia*.

Collins (1973) found that Munz's 1930 description and illustration of the corolla lobes of *O. ludoviciana* did not match the morphology of Nuttall's type specimen. The corolla lobes of the type specimen are rounded on both the upper and lower lips, but Munz's illustration, based on a specimen from White County, Illinois, shows a corolla with triangular-pointed lobes. Because Munz used material that matched his illustration in assembling his description of *O. ludoviciana*, subsequent regional and state floras continued to overlook the morphological heterogeneity between populations attributed to that species.

Repeated and extensive examination of specimens of *O. ludoviciana* sensu stricto from its entire geographic range has revealed that the character of rounded corolla lobes is consistent throughout for upland plants (Fig. 1). In contrast, the corolla lobes of bottomland plants, hereafter referred to as *O. riparia*, are consistently triangular and pointed (Fig. 1). The populations of *O. riparia* share several additional characteristics (Table 1): 1) They are found almost exclusively in river bank and sandbar habitats in floodplains; 2) The native hosts are annual members of Asteraceae tribe Heliantheae, subtribe Ambrosiinae, primarily *Ambrosia trifida* L. and *Xanthium strumarium* L., and occasionally *Ambrosia artemisiifolia* L. and *Dicoria canescens* A. Gray 3)

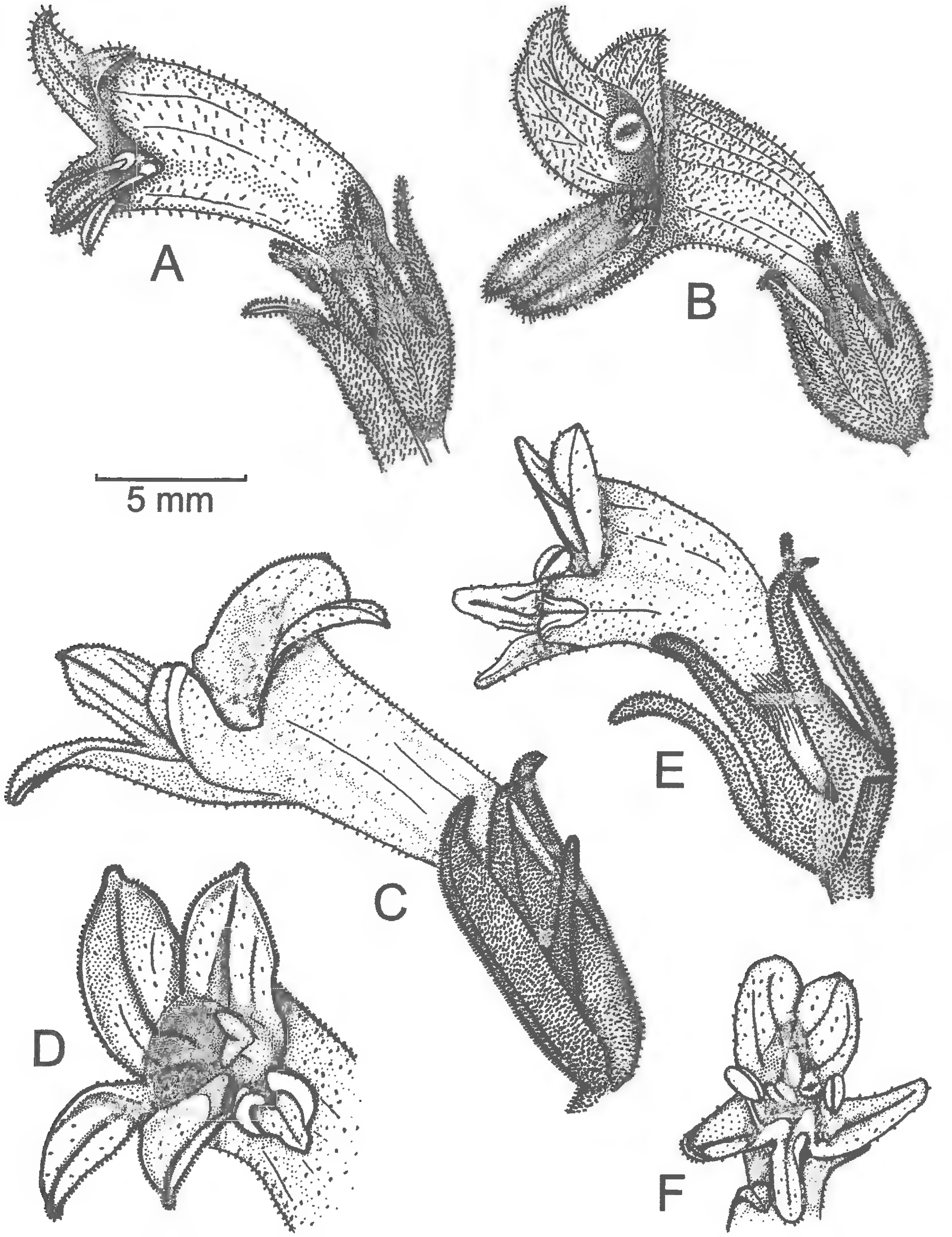

Fig. 1. Comparative illustrations of corollas of three species of *Orobanche*. A, B) *O. riparia*; A) eastern form, B) western form. C, D) *O. cooperi*. E, F) *O. ludoviciana*.

Table 1. Comparison of selected characters of three species of *Orobanche*: *riparia*, *ludoviciana*, and *cooperi*.

Character	*Orobanche riparia*	*Orobanche ludoviciana*	*Orobanche cooperi*
Calyx length	7–11 mm	8–14 mm	7–12 mm
Corolla length	15–22 mm	14–20 mm	15–32 mm
Shape and size of corolla lips/lobes	Triangular-acute, 4–5mm, erect or slightly reflexed	Rounded-obtuse, 4–8mm, erect or ascending	Triangular-acute, 5–8 mm, apiculate apex, ascending or reflexed
Corolla tube	Strongly curved, tube horizontal slightly flared distally	Slightly curved, tube ascending, slightly flared distally	Strongly curved, tube ascending, flared distally
Corolla color	Pallid, or upper lobe apex purple/lavender	Purple, lavender, rose, or pallid, tube exterior whitish	Dark purple on distal half with white exterior and throat
Pubescence	pubescent with glandular and eglandular trichomes or glabrate	Pubescent with glandular trichomes except inner lobe surface	Pubescent with glandular trichomes on tube, eglandular on inner surface of lobes
Flowering	August–October	April–August	December–April
Inflorescence arrangement	Open raceme, flowers in loose, regular spiral on floral axis	Compact raceme, flowers in dense, often irregular spiral on floral axis	Open or compact raceme with flowers in loose, regular spiral on floral axis
Primary hosts	Annuals; *Ambrosia, Xanthium, Dicoria*	Perennials; *Grindelia, Artemisia, Heterotheca*	Perennials; *Ambrosia*
Habitat and main range	River banks, sandbars eastern U.S. and prairie provinces	Prairie, desert, dunes; central and western U.S.	Sonoran Desert, ravines, dry stream beds, dunes; southwestern U.S.

The flowering period is from mid-August to early October; 4) Inflorescence color is typically pallid with only the interior tips of the corolla lobes tinted purple; 5) The corolla tube is strongly curved with the distal portion of the tube horizontal, slightly flared distally, and palatal folds that are either glabrous or densely pubescent.

Compared with *O. riparia*, *O. ludoviciana* has slightly shorter corollas with a flared throat and rounded corolla lobes (Table 1). It occurs mainly through the Great Plains (and eastward along the Prairie Peninsula) in various habitats, including sandy prairies, sand dunes, dry washes, calcareous (caliche) soils, and lower slopes of the Rocky Mountains. Its hosts are almost exclusively perennial members of Asteraceae tribes Astereae and Anthemideae, including *Grindelia squarrosa* (Pursh) Dunal, *Heterotheca* spp., *Artemisia* spp., and occasionally other genera. The principal flowering period is from late April in the southern plains through mid-August in the northern plains, although sporadic flowering has been observed rarely at other times in marginal habitats. The corolla tube is slightly curved at the constriction, ascending, and flared distally, with the palatal folds sparsely pubescent. Floral pigmentation varies from purple to pale rose and occasionally yellow, usually with dark purple upper lobes (Table 1).

Additionally, populations of *O. riparia* are ecologically and somewhat geographically distinct, and the habitat distinction is maintained in the western populations, where the two ecological races are geographically somewhat sympatric. Populations east of the Mississippi River (but including Missouri) are allopatric with *O. ludoviciana*. West of the Mississippi River, sympatry of the two species occurs from eastern Nebraska and Kansas to eastern Colorado, southward into New Mexico and the Texas Panhandle. A small overlap in flowering times in early August could provide an opportunity for hybridization between the two species. Although no suspected cases of hybridization have been observed based on morphology or field observations of populations, more definitive data from genetic studies are needed to answer this question. Molecular studies by Colwell are currently underway.

Munz (1930) treated *O. cooperi* as a variety of *O. ludoviciana*, but subsequent authors mostly have accepted it as a separate, but closely related species (Shreve & Wiggins 1964; Munz 1974). *Orobanche cooperi* is

distinguished by its dark purple color, larger, ascending corolla tube, and erect or strongly reflexed, triangular lobes with apiculate apices. The corolla tube has a white exterior and is slightly curved and flared distally, with palatal folds pubescent at the mouth and becoming glabrous in the throat. The habitat is primarily Sonoran Desert scrub, often associated with washes that remain dry except in monsoon season. Its hosts are shrubs in various tribes of Asteraceae, principally species of *Ambrosia* and *Encelia* (all Heliantheae, Ambrosiinae), but also reported on *Gutierrezia* (Astereae). The flowering period is mainly December through April (Table 1). Collins (1973) found that the cross-sectional stem anatomy of *O. cooperi* and *O. riparia* are very similar and that *O. ludoviciana* differs significantly from both of the other taxa.

Several characters suggest that *O. riparia* is more closely related to *O. cooperi* than to *O. ludoviciana*. *Orobanche riparia* and *O. cooperi* share an affinity for riparian or water-eroded habitats and hosts in the subtribe Ambrosiinae. They differ in that *O. cooperi* occurs only in seasonally arid habitats, whereas *O. riparia* occurs in both mesic and semi-arid habitats, and that the former parasitizes shrubby hosts, whereas the host taxa of the latter are annuals. The pubescence of the corolla lobes in both species is eglandular on the inner surface with vestiture considerably longer than the short glandular trichomes typical of the exterior surface. Likewise, the palatal folds are invested with eglandular trichomes, differing between the species only in their distribution on the folds. This shared pattern of trichomes is more evident in the western populations of *O. riparia* than in the eastern populations. Similarly, the eastern populations have reduced indumentum as compared with the western populations. One can speculate that *O. riparia* and *O. cooperi* share a recent common ancestor. A possible scenario is that a progenitor's range became bisected, with populations that became *O. riparia* adapting and dispersing into new habitats eastward across the American Midwest and populations now referable to *O. cooperi* attaining a distribution in the southwestern U.S. and adjacent Mexico. If this is the case, *O. riparia* adapted quickly to annual hosts and a late summer to early fall flowering period, in contrast with the shrubby hosts and late winter to early spring flowering period of *O. cooperi*. Of this character set, *O. ludoviciana* shares only the semi-arid habitat and perennial hosts with *O. cooperi*, although the host taxa of *O. ludoviciana* often are herbaceous.

Orobanche riparia L.T. Collins, sp. nov. (**Fig. 1**). Type: UNITED STATES: Indiana: Gibson Co.: common on bank of slough, ca. 2.5 mi N of Griffin, 16 Aug 1931, *Deam 50941* (holotype: IND; isotypes: A, F, GH, IND, MINN, WIS).

Ab *O. ludoviciana* differt lobis corollae apice acutis, puberulis vel pubescentibus, tubo horizontali, constricto flexoque super ovarium, inflorescentia laxe racemosa. Ab *O. cooperi* differt corolla 15–22 mm longa, lobis corollae apice nec apiculatis nec reflexis, inflorescentia pallide purpurea.

Annual root parasite, lacking chlorophyll. Coralloid roots few, rudimentary, stout, fleshy, usually forming a single host attachment. Stem stout or slender, fleshy, 5–35 cm long, mostly subterranean, solitary or clustered, unbranched or more commonly branched from near base with a few to rarely numerous branches, each bearing a terminal inflorescence; stem base irregularly enlarged or not, 5–20 mm in diameter; glabrous, creamy white, yellow, or tan, drying ferruginous, dark brown, or black. Leaves reduced to scales, 7–10 mm long, cauline, spirally alternate, appressed, broadly ovate to ovate triangular, becoming narrower distally. Inflorescence an open spike-like raceme, glandular pubescent; bracts mostly ca. 1 cm long, the distal ones shortened, narrowly oblong-lanceolate, acute at the tip, pale lavender to dark purple. Flowers sessile or the proximal ones on short pedicels, evenly and spirally inserted on the axis, subtended by 2 small, linear-subulate bracteoles; calyces 7–11(–13) mm long, purple, deeply 5-lobed, the lobes lance-linear to linear-subulate, about equal in length, densely glandular pubescent; corollas (13–)15–22 mm long, constricted above the ovary, strongly curved at the constriction, the tube nearly horizontal, exterior surface glandular puberulent or pubescent, persistent, the tube narrow or slightly flared distally, cream-white sometimes tinted with purple, the throat with yellow palatal folds, glabrous or pubescent on folds and in grooves with eglandular trichomes; upper lip ca. 5 mm long, erect, divided about half its length, the 2 lobes triangular-acute, lavender or purple, puberulent or densely pubescent with eglandular trichomes; lower lip 3–4 mm long, divided to its base into 3 linear lobes with an acute apex, ca. 1 mm wide, pubescent with eglandular trichomes, pale, often with 1–3 purple veins. Stamens 4, inserted on the corolla tube at its constriction, generally glabrous

or with a few scattered hairs, anthers ca. 1 mm long, white, glabrous or sparsely pubescent, equalling or shorter than style. Ovary somewhat asymmetrically ovoid, 2-carpellate, nectary not evident; placentation parietal, with 4 lateral placentae; style filiform, equaling the corolla tube or shorter, stigma peltate, discoid-crateriform or rarely somewhat 2-parted Fruits 2-valved capsules, 0.7–1 cm long; seeds numerous, 0.3–0.5 mm long, ovoid to broadly ellipsoid, reticulate-pitted, light tan to dark brown. $2n = 48$ (Collins 1973). Flowering mid-August to early October.

The species ranges (Fig. 2) from the Potomac and Shenandoah River valleys of Virginia to southern Ohio and Indiana along the Ohio River to Central Illinois along the Wabash and Sangamon Rivers, to the Meramec River in eastern Missouri (near St. Louis), southward to a tributary of the Mississippi River in western Tennessee, and westward along the Platte River in Nebraska and Eastern Colorado. Some apparently isolated populations occur in the Kansas, Oklahoma, Texas, and New Mexico along the Canadian, Cimarron, and Rio Grande rivers and their tributaries. Only historical collections are currently known from the District of Columbia, Virginia, and West Virginia. The species is found entirely on mixed sand and silt deposits on stream banks of eastern rivers or on sandbars or sandy banks of western rivers. Hosts are *Ambrosia trifida* and *Xanthium strumarium*, and occasionally *Ambrosia artemisiifolia* and *Dicoria canescens*. Rarely reported alternate hosts are *Nicotiana tabacum* L. and *N. glauca* Graham.

Representative specimens: **UNITED STATES. COLORADO: Crowley Co.:** cultivated field near Ordway, 22 Jul 1948, *Wilchusen s.n.* (CS). **Jackson Co.:** N sandhills E of Cowdry, 1 Oct 1982, *Wilken 13922* (CS). **Logan Co.:** cultivated field [along Platte River] near Sterling, *anonymous*, 8 Sep 1965 (CS). **Prowers Co.:** sandy bed of Butte Creek, 6 mi E of Two Buttes Peak, 24 Aug 1964, *Martin s.n.* (COLO, CS). **Weld Co.:** sandhills 3 mi NE of Roggen, 1 Sep 1972, *Maslin s.n.* (COLO, CS). **DISTRICT OF COLUMBIA:** E end of New Long Bridge, 2 Sep 1905, *Ward s.n.* (US). **ILLINOIS: Cumberland Co.:** banks of Embarras River, 2 mi E of Greenup, 18 Sep 1980, *Collins 1618* (MO). **Mason Co.:** bank of Salt Creek and edge of cornfield, 5 mi N of Greenview, 15 Sep 1980, *Collins 1615* (MO). **Menard Co.:** bottoms, Athens, 1860, 1861, 1866, 1867, *E. Hall s.n.* (F, GH, IL, MO, POM, WIS). **Wabash Co.:** S of Mt. Carmel along banks of Wabash River and Greathouse Creek, 18 Sep 1980, *Collins 1619* (MO). **INDIANA: Harrison Co.:** W of landing at Mauckport, 25 Aug 1945, *Deam 63566* (IND). **Jefferson Co.:** tobacco field 0.5 mi E of Brooksburg, 15 Sep 1935, *Banta s.n.* (IND). **Knox Co.:** along ditch 2 mi N of Decker, 9 Oct 1938, *Deam 59255* (IND). **Posey Co.:** E bank of Wabash River at New Harmony, 28 Aug 1971, *Collins 1555* (MO, WIS). **Sullivan Co.:** roadside S of Busseron Creek, 6.5 mi SW of Carlisle, 1 Sep 1939, *Deam 59424* (IND). **Vandenburgh Co:** river slough, 17 Oct 1941 *Zeiner s.n.* (IND), **Warrick Co.:** banks of Ohio River at Newburg, 28 Aug 1971, *Collins 1543* (UWM). **KANSAS: Allen Co.:** Iola, Sep 1925, *anonymous* (KSC). **Greenwood Co.:** potato patch near Eureka, 24 Sep 1935, *Farmer s.n.* (KS). **Morton Co.:** Cimarron River bed N of Wilburton, Aug 1929, *Gates 16205* (F, KSC, MO). **KENTUCKY: Pendleton Co.:** Ohio River bank at Ivor, 27 Nov 1942, *Chicoine 4745* (MO, US). **MISSOURI: St. Louis Co.:** exposed gravel bar on S bank of Meramec River, 2 mi N of Crescent, 1 Sep 1991, *Yatskievych & Colwell 91-195* (MO). **NEBRASKA: Buffalo Co.:** sandbar in Platte River, 2 mi S of Odessa, 8 Oct 1999, *Collins 1620* (MO, WTU). **Cass Co.:** sandbar in Platte River, 2 mi NE of Louisville, 15 Sep 1934, *Morrison 1342* (NEB). **Dawson Co.:** sandbar in Platte River, S of Lexington, 8 Oct 1999, *Collins 1621* (MO). **Kearney Co.:** sandbars of Platte River, Minden, 15 Sep 1922, *Hapeman s.n.* (PH, POM/RSA, WTU). **Lincoln Co.:** sandbar in Platte River, Sutherland, 13 Aug 1936, *anonymous* (NEB). **Merrick Co.:** sandbar in Platte River, near Central City, 22 Aug 1938, *I. Mueller s.n.* (NEB). **NEW MEXICO: Doña Ana Co.:** sand, Mesilla Valley, 25 Aug 1906, *Wooten & Stanley s.n.* (US). **Sandoval Co.:** sandy soil, Arroyo Chico, 22 Sep 1973, *Bohrer 1758* (ARIZ). **San Juan Co.:** low sand dunes on Chaco River, 30 m S of Farmington, pipeline right-of-way on BIA Road 2, 4 sep 2007, *Collins & Heil 2032* (MO). **Socorro Co.:** sand along Rio Grande, San Marcial, 1 Aug 1897, *Herrick 825* (US). **Union Co.:** idle field, 17.5 mi SW of Clayton, 1 Sep 1936, *Cogdell 125* (GH). **OHIO: Clermont Co.:** 0.5 mi E of Chilo, 20 Oct 1949, *Bartley s.n.* (OS, US). **Hamilton Co.:** mouth of little Miami River, 25 Sep 1934, *Haller s.n.* (US). **Scioto Co.:** Nile Township along Ohio River, 29 Aug 1949, *Roth s.n.* (GH). **OKLAHOMA: Cleveland Co.:** sand in bed of Canadian River, 10 mi NW of Norman, 8 Sep 1946, *Goodman 4078* (MO). **TENNESSEE: Lauderdale Co.:** along roadway at mouth of Lower Forked Deer Creek, ca.2 m NE of Ashport, 16 Oct 1972, *Piehl s.n.* (TENN). **TEXAS: Brewster Co.:** Boquillas Canyon, Chisos Mts., sand near Rio Grande River bank, 5 Aug 1937, *Warnock* 838 (ARIZ, TEX, US). **Dallam Co.:** sandy soil, Rita Blanca Creek N of Dalhart, Aug 1949, *York & Rogers 233* (OSU, TTC). **El Paso Co.:** vicinity of El Paso, 1911, *Stearns* 40 (MO, US). **Hartley Co.:** deep sand on creek bank, Punta del Agua Creek 30 mi SW of Dalhart, 26 Sep 1965, *Collins* 821 (OSU, TTC). **Wheeler Co.:** 5 mi S & 7 mi E of Miami, Jul 1967, *Baggerman s.n.* (TTC, WIS, UWM). **VIRGINIA: Campbell Co.:** 8 mi from Lynchburg, 13 Oct 1933, *Freer s.n.* (US). **Page Co.:** banks of Shenandoah River, Luray, 22 Aug 1912, *Holtzman s.n.* (US). **Warren Co.:** sandy field, Front Royal, 18 Sep 1897, *Miller s.n.* (US). **WEST VIRGINIA: Summers Co:** New River, above Shanklin's Ferry, 23 Aug 1946, *McNeill s.n.* (WVA).

Eastern and western populations have an apparent disjunction in distribution between eastern Missouri and east central Nebraska, a distance of ca. 650 km. A full list of specimens examined is available upon request to the authors. It is uncertain whether this is a true disjunction or simply the lack of intensive field work in this region to locate obscure populations (many botanists avoid botanizing in the midst of dense

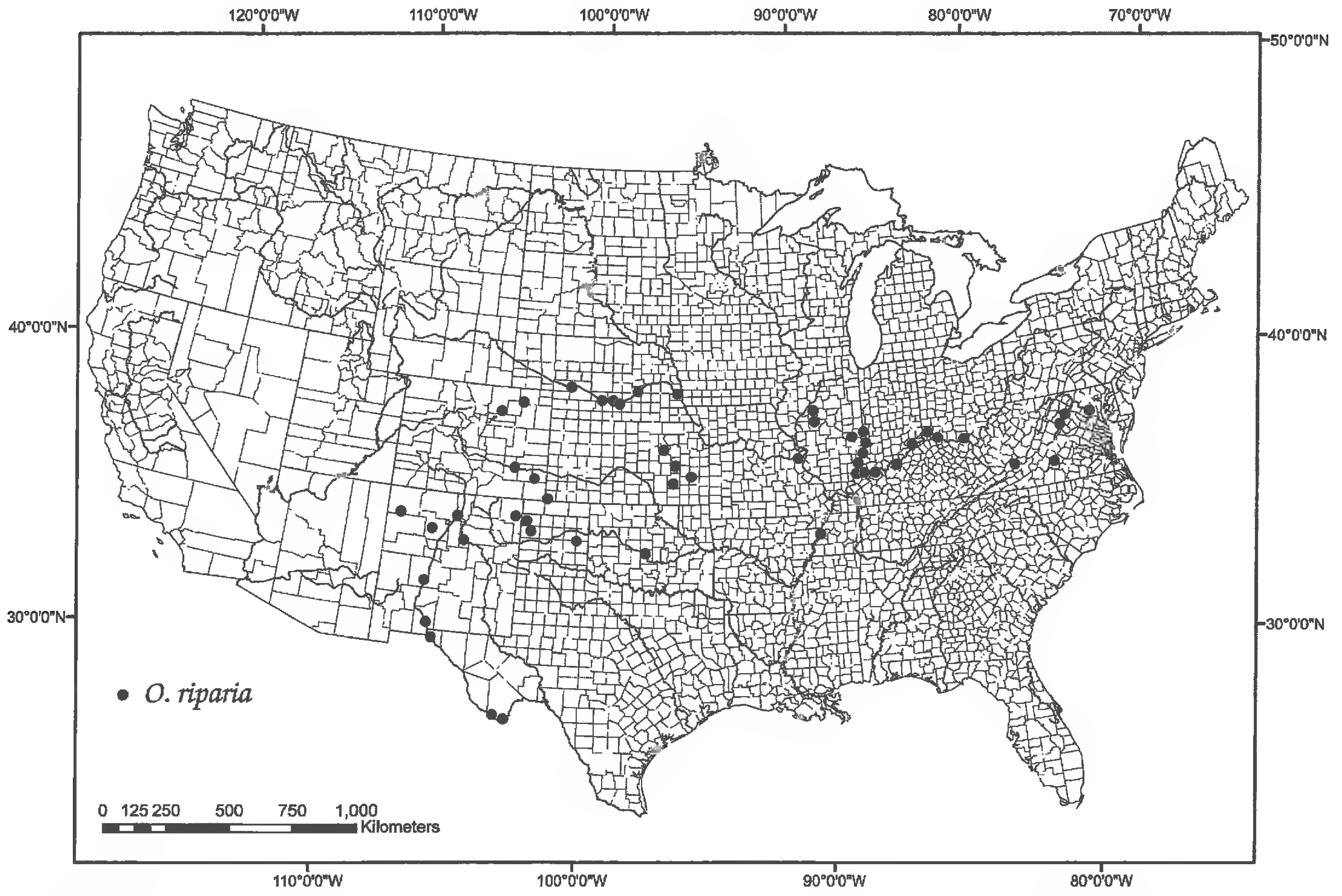

Fig. 2. Distribution of *Orobanche riparia*.

stands of ragweed and cocklebures during allergy season). The eastern and western populations of *O. riparia* exhibit slightly different morphologies. Plants of the eastern populations (including the Missouri plants) are generally pallid with very pale lavender or purple pigmentation in the corollas. Pubescence is reduced and sometimes almost absent, especially on the corolla lobes. The primary host is *Ambrosia trifida*. The habitat of these populations is floodplains with mixed sand and heavy silty loam soils of the midwestern rivers cited above.

The western populations (west of eastern Missouri) have more deeply purple-tinted corolla lobes, calyx lobes, and floral bracts. The upper stems, where exposed to sunlight, may be infused with a rosy purple. Pubescence is rather dense on the inflorescence, corolla lobes, and palatal folds. The primary host is *Xanthium strumarium*. Populations of this variant are concentrated along sand bars of the Platte River in Nebraska, with a few records of populations widely scattered in Kansas, Oklahoma, Texas, Colorado, and New Mexico. Specimens of this species collected along the Rio Grande River from central New Mexico to the Big Bend of Texas have proven problematic for identification throughout the study of Section *Nothaphyllon*. Only recently, when they were compared with the Nebraska plants, did it become apparent that they represent populations of *O. riparia*.

It is tempting to name these two variants formally as subspecies within *O. riparia*. However, the life history and morphological distinctions are not sufficient to warrant taxonomic status at this time. This problem requires more intensive study of both morphological and genetic variation within and between populations before a conclusion can be reached as to the merits of segregating infrataxa within *O. riparia*.

Host information for *Orobanche* is generally difficult to assess from herbarium labels. Collectors sometimes list as a host any adjacent plant without confirming a physical connection or list no host at all. However, host data for *O. riparia* reported here have been observed by all three authors. Only two non-Asteraceous

host reports have been confirmed. Some populations in southern Ohio occasionally parasitize cultivated tobacco (*Nicotiana tabacum*). Likewise, some populations along the Rio Grande in western Texas have been reported on the weedy, introduced *N. glauca* (the only perennial host with which the species has been associated). It is not possible at this time to judge the significance of these exceptions, if any. Anecdotal evidence suggests that other species of *Orobanche* sometimes utilize anomalous alternate hosts at the margins of their ranges.

The populations east of the Appalachian Mountains are of particular interest because they represent the extreme eastern portion of the range and may possibly be extirpated. Virginia records are represented by four herbarium specimens from four counties (on the James, Shenandoah and Potomac rivers). The most recent collection we have seen was made in 1933. A single specimen was seen from the New River, Summers County, West Virginia. The present study could not confirm extant populations in the District of Columbia, Virginia, or West Virginia. The species seems reasonably secure elsewhere in its range, although current herbarium vouchers document a highly fragmented range. For example, the single Tennessee record represents a southward disjunction of ca. 325 km from the St. Louis County, Missouri station. However, field experience of the authors suggests that this species is probably more common than the herbarium records indicate. The senior author discovered several previously unreported populations in Nebraska, Illinois, and Indiana. Additionally, a few populations were observed in Illinois, Ohio, and Texas that were located on minor tributaries (creeks) of the major river systems. Some of the historical populations were determined to be extant. Thus, it is likely that concentrated field work will reveal additional populations of *O. riparia*. The status of the historical populations in the District of Columbia, Virginia, and West Virginia especially needs to be updated by further field work.

The habitat of *O. riparia* is disturbed annually by natural events and human activity. Although it is widely distributed, populations seem to be locally isolated and therefore fragile. The senior author has observed the obliteration of a large population in Posey County, Indiana, as a result of riverbank development. Because of its unique distribution of widely separated populations in regularly disturbed habitats, the species is likely to be threatened on a local or state basis.

ACKNOWLEDGMENTS

The authors wish to express their appreciation to the staff and curators of the following herbaria for the loan of specimens and/or for providing images and label data from specimens in the *Orobanche riparia* alliance: A, ARIZ, COLO, CS, F, GH, ILL, IND, JEPS, KS, MICH, MIN, MO, NEB, NY, OSC, OKLA, PH, POM, RSA, TENN, TTC, UC, US, UWM, WIS, WTU, and WVA. Collins is grateful to Ken Heil (San Juan College) for accompanying him during field work in the southwestern U.S. Financial support for some of the field work of Collins was provided by a grant from the Evangel University Faculty Summer Research Program. Colwell's initial contributions to this project during her doctoral studies in St. Louis were supported by the Department of Biology at Washington University. The Flora of North America Project additionally provided funding for one of Colwell's trips to the Missouri Botanical Garden.

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BOOK REVIEW

Stephen Ingram. 2008. **Cacti, Agaves, and Yuccas of California and Nevada.** (ISBN 978-0-9789971-0-6, pbk.; 978-0-9789971-1-3; hbk.). Cachuma Press, P.O. Box 560, Los Olivos, California 93441, U.S.A. (**Orders:** www.cachumapress.com, 805-688-0413). $25.95 pbk., $35.95 hbk., 256 pp., 262 color photographs, 16 botanical watercolors, 52 range maps, 6 3/4" × 9 1/4".

What a beautifully illustrated book! The cover stock for the gatefold cover is 14 point with the binding Smythsewn. The text paper is "Lumi gloss," acid free, and 150 gsm weight. The front cover surface should protect against liquid stains when in the car, wear and tear when carried in a book bag, or from ground debris when in use while doing groundwork.

The paperback version is small and durable enough to carry into the field on camera shoots or collecting forays and large enough so that color images of landscapes show scenic vistas, habitats that characterize the desert ecosystem, and morphological details of individual plants, plant parts, and flowers. The printing of this book has captured the rich colors and hues in the high-resolution photographic images that are displayed as full page or two-page layouts. The landscapes show extraordinary depth of field with cacti in the foreground and mountain ranges in the background and both in focus.

One color image is an outstanding example of Ingram's spectacular photography and is represented by a two-page (176–177) layout that reminds me of Ansel Adams's most famous photograph "Moonrise, Hernandez, New Mexico, 1941" where the fast fading twilight and moonrise involved a magic moment to make a picture that will forever rank as one of the finest black and white images in the history of photography. Substitute the twilight illumination of Parry's nolina flower stalks for Adams's tombstones and the Little San Bernadino Mountains for the Sangre de Cristo Mountains, and you have a color image that is a magic moment. There are a number of magic moments in this book.

The author spent many years traveling more than 30,000 miles on backroads to be at the right place at the right time to take advantage of the ephemeral cactus flowers that have a brief phenological window. Ingram lives on the eastern slope of the Sierra Nevada in the heart of the porcupine prickly-pear habitat. A sense of place becomes part of the areas documented in this book such as the Great Basin Desert, Mojave Desert, and Colorado Desert (part of the Sonoran Desert). The intent of the author is to span the readership from the general public, naturalist, and expert, and increase the appreciation of native plants to enhance conservation, and he deserves five stars for surpassing the highest standards.

This book is divided into five chapters: (1) Evolution, Classification, and Botanical Characteristics; (2) Ecology and Habitats of Cacti, Agaves, and Yuccas; (3) Species Profiles; (4) Conservation and Cultivation; and (5) Exploring the Cactus Country of California and Nevada. The eight appendices are especially informative and increase the value of the book: Cactus, Agave, and Yucca Species of California and Nevada; Major Vegetation Types and Habitats for Cacti, Agaves, and Yuccas; Scientific Names of Non-featured Species; Cholla Species Comparison; Prickly-pear Species Comparison; Species Rarity Status; Education, Conservation and Cultivation Resources; Species List for Selected Public Lands in California and Nevada.

The species profiles for each entry include the common name, the scientific name, a phonetic pronunciation guide, recent synonyms, other common names, a commentary about the plant, a landscape, habit, and flower photograph plus a range map. Identifying characteristics include descriptions of the habit, stems, spines or leaves, flowers, and fruits as appropriate for the species. The chapter on "Conservation and Cultivation" is especially noteworthy since the information—on conservation practices, illegal harvest, cultivation (landscape species), growing plants in containers and gardens, and propagation—will have broad appeal to homeowners and gardeners. The section on "Exploring the Cactus Country of California and Nevada" lists the specific sites where selected species can be found on public lands such as reserves, state parks, national parks, national preserves, wilderness areas, wildlife refuges, and recreation areas.

Sections that aid in using this book as an educational resource to identify common, indigenous, rare, and possibly new species are the excellent key to the genera and a glossary that defines the terminology used in the book. The 15 genera of Cactaceae and Agavaceae that occur in California and Nevada are represented by the famous watercolor paintings by Eugene O. Murman and three by Susan Bazell. The use of sidebars add related factual details that enliven the text. For example, "Packrat Middens and Vegetation History" and "Yuccas and Yucca Moths" in both cases add to the curiosity associated with these plants, especially the yucca moth-flower pollination biology often featured in biology textbooks as obligate mutualism.

Although the references are not cited in the text, the Bibliography has more than 200 citations mostly published in the last ten years. Web sites are also included for additional information. The Index assists the reader by including common names, scientific names by genus and species listed afterwards, national and state parks, and persons of interest.

This book must be on the bookshelf of every library, botanist, ecologist, horticulturist, gardener, landscaper, conservationist, botanical museum, and herbarium and should be available as a textbook for special seminars on the desert ecosystem and at state parks and national parks especially in Western states. Cachuma Press, the editors, and author are to be commended for producing a book that will be cherished by all bibliophiles!—*Harold W. Keller, Ph.D., Research Associate, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

BRISTLECONE PINE DWARF MISTLETOE: *ARCEUTHOBIUM MICROCARPUM* SUBSP. *ARISTATAE* (VISCACEAE), A NEW SUBSPECIES OF WESTERN SPRUCE DWARF MISTLETOE FROM NORTHERN ARIZONA

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ABSTRACT

We describe **Arceuthobium microcarpum** subsp. **aristatae** (Viscaceae), a parasite of bristlecone pine (*Pinus aristata* Engelm.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in northern Arizona. Morphological and phenological data were used to compare *A. microcarpum* populations parasitizing bristlecone pine on the San Francisco Peaks, Arizona, with populations on Engelmann spruce and blue spruce (*Picea pungens* Engelm.) from other locations in Arizona and New Mexico. Morphological, phenological, and host susceptibility differences support the classification of the populations of *A. microcarpum* on the San Francisco Peaks and Kendrick Peak in northern Arizona as a new subspecies.

RESUMEN

Se describe **Arceuthobium microcarpum** subsp. **aristatae** (Viscaceae), un parásito de *Pinus aristata* Engelm. y de *Picea engelmannii* Parry ex Engelm. en el norte de Arizona. Se usaron datos morfológicos y fenológicos para comparar poblaciones de *A. microcarpum* que parasitan a *Pinus aristata* de San Francisco Peaks, Arizona, con poblaciones que parasitan a *Picea engelmannii* y a *Picea pungens* Engelm. en otras localidades de Arizona y Nuevo México. Diferencias morfológicas, fenológicas y de susceptibilidad de los hospedadores fundamentan la clasificación de las poblaciones de *A. microcarpum* de San Francisco Peaks y de Kendrick Peak en el norte de Arizona como una subespecie nueva.

Key Words: *Arceuthobium, Picea engelmannii, Picea pungens, Pinus aristata,* Arizona

Western spruce dwarf mistletoe (*Arceuthobium microcarpum* (Engelm.) Hawksw. & Wiens) is an important parasite of blue spruce (*Picea pungens* Engelm.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in the southwestern United States (Mathiasen et al. 1986; Hawksworth & Wiens 1996). It occurs as far south as the Pinaleño Mountains, Arizona and Sacramento Mountains, New Mexico and as far north as the Kaibab Plateau, Arizona. However, western spruce dwarf mistletoe is most common in the White Mountains, Arizona and Mogollon Mountains, New Mexico (Mathiasen et al. 1986; Hawksworth & Wiens 1996). On the San Francisco Peaks, Arizona, it also parasitizes Rocky Mountain bristlecone pine (*Pinus aristata* Engelm.) (Mathiasen & Hawksworth 1980). Initially, the dwarf mistletoe infecting bristlecone pine on the San Francisco Peaks was classified as limber pine dwarf mistletoe (*Arceuthobium cyanocarpum* (A. Nelson ex Rydb.) Coulter & Nelson) by Hawksworth and Wiens (1972). It was later classified as *A. microcarpum* based on its host affinities and chemical characters (flavonols) (Crawford & Hawksworth 1979; Mathiasen & Hawksworth 1980; Hawksworth & Wiens 1996). Although Mathiasen and Hawksworth (1980) reported morphological, phenological, and host susceptibility differences between the *A. microcarpum* populations on the San Francisco Peaks and other *A. microcarpum* populations in the Southwest, they did not recommend giving the San Francisco Peaks populations taxonomic status at that time. In 2006, we began a more detailed analysis of the morphological characteristics of the *A. microcarpum* populations in Arizona. Our data further substantiated the differences between the *A. microcarpum* populations on the San Francisco Peaks and those in other mountain ranges of Arizona first reported by Mathiasen and Hawksworth (1980). Because of the differences in plant size, plant color, phenology, host affinities, and geographic isolation of

the dwarf mistletoe populations on the San Francisco Peaks, and nearby Kendrick Peak, there is sufficient evidence to describe these populations as a new subspecies of *A. microcarpum*.

Arceuthobium microcarpum (Engelm.) Hawksw. & Wiens subsp. **aristatae** J.M. Scott & Mathiasen, subsp. nov. (**Figs. 1–2**). Type: U.S.A. Arizona. Coconino Co.: near summit of Schultz Peak, a southeast subsidiary ridge of the San Francisco Peaks, Coconino National Forest, elev. 3,060 m, Lat. 35° 18' 43" N, Long. 111° 37' 52" W, parasitic on *Pinus aristata*, 8 Aug 2006, *J.M. Scott 2006-6* (holotype: ASC; isotypes: JEPS, UNM, US).

Plantae (1–)3(–7) cm altae; surculi principales basi (1–)1.8(–3) mm diam; fructus maturi 3.3 × 2.1 mm; anthesis mense Julio–Augusto; fructus maturitas Augusto–Septembri; in *Pinus aristata* et *Picea engelmannii* parasiticae.

Male plants (0.8–)2.7(–7.0) cm in height, basal diameter of dominant plants (1.0–)1.8(–3.0) mm; female plants (1.4–)3.6(–7.0) cm in height, basal diameter of dominant plants (0.6–)1.8(–3.0) mm; male and female plant plants primarily light green, but some brown-green or purple; male flower diameter 2.5 mm, perianth lobe dimensions 1.2 × 1.0 mm, anther diameter 0.5 mm, distance from anther to perianth tip 0.5 mm; fruit dimensions 3.3 × 2.1 mm; seed dimensions 2.4 × 1.1 mm.

Common name.—bristlecone pine dwarf mistletoe.

Etymology.—We selected *aristatae*, a name that indicates the principal host of this dwarf mistletoe is *Pinus aristata*.

Phenology.—Anthesis from early July to late-August with peaks in late-July to early-August; seed dispersal from mid-August to late-September with peaks in mid- to late-August to early-September.

Habit.—Parasitic principally on *Pinus aristata* and occasionally on *Picea engelmannii* on Schultz Peak, parasitic principally on *Picea engelmannii* in the Inner Basin of the San Francisco Peaks and on nearby Kendrick Peak. Not known on *Picea pungens*. Rarely infects *Pinus flexilis* James and *Abies lasiocarpa* (Hook.) Nutt. on Schultz Peak.

Distribution.—Bristlecone pine dwarf mistletoe only occurs in three small populations on the San Francisco Peaks (Schultz Peak, Weatherford Trail, and Inner Basin, Fig. 3). It also occurs near the summit of Kendrick Peak (Fig. 4). It ranges in elevation from 2890 to 3130 m on Schultz Peak.

METHODS

Collection Locations.—In 2006 and 2007, plants of *A. microcarpum* were collected from 18 populations in Arizona (Appendix A; Appendices A–F available online at http://www.for.nau.edu/SOFArchive/MSF-Students/JMScott/20090325.pdf). Four populations were sampled near Flagstaff, Arizona (host plants): Schultz Peak (bristlecone pine and Engelmann spruce), Weatherford Trail (bristlecone pine), Inner Basin (bristlecone pine and Engelmann spruce) (Fig. 3), and Kendrick Peak (Engelmann spruce) (Fig. 4). A total of 12 populations of *A. microcarpum* were sampled in the White Mountains (host plants): Cache Cienega (blue and Engelmann spruce), Coleman Creek (blue spruce), Hannagan Creek (blue spruce), Johns Canyon (blue spruce), Lee Valley (blue spruce), Williams Valley (blue spruce), Forest Road 249 (blue spruce), Forest Road 402 (blue and Engelmann spruce), and Forest Road 72 (blue and Engelmann spruce) (Fig. 4). In addition, two populations were sampled from the North Rim of the Grand Canyon: Point Royal Road (blue spruce) and Route 67 (blue spruce).

In 1975 and 1976, plants of *A. microcarpum* were collected by the junior author from the same locations and hosts on the San Francisco Peaks that were sampled in 2006–07. Plants were also collected from the North Rim of the Grand Canyon (blue spruce), the White Mountains (blue and Engelmann spruce), the Mogollon Mountains (blue spruce), and the Pinaleño Mountains (Engelmann spruce) (Fig. 4).

Morphological Measurements.—The following morphological characters of male plants were measured: dominant plant height, dominant plant basal diameter, flower diameter, anther diameter, perianth lobe length, perianth lobe width, and distance from the outer edge of the anther to the tip of the perianth lobe. The following morphological characters were measured for female plants: dominant plant height, dominant plant basal diameter, length and width of both fruits and seeds. The color of plants, fruits, and seeds were recorded. Plant heights and basal diameters were measured with digital calipers to the nearest 0.1 cm. All

Fig. 1. Holotype of *Arceuthobium microcarpum* subsp. *aristatae* J.M. Scott & Mathiasen, subsp. nov., *J.M. Scott 2006-6*, 8 Aug 2006 (ASC). Photo by R.L. Mathiasen.

Fig. 2. (Top) Male *Arceuthobium microcarpum* subsp. *aristatae* infecting *Picea engelmannii* in the Inner Basin of the San Francisco Peaks, Arizona. Photo taken on 27 May 2008 by J.M. Scott. (Bottom) Male *Arceuthobium microcarpum* subsp. *aristatae* infecting *Pinus aristata* on Schultz Peak, Arizona. Photo taken 30 May 2008 by J.M. Scott.

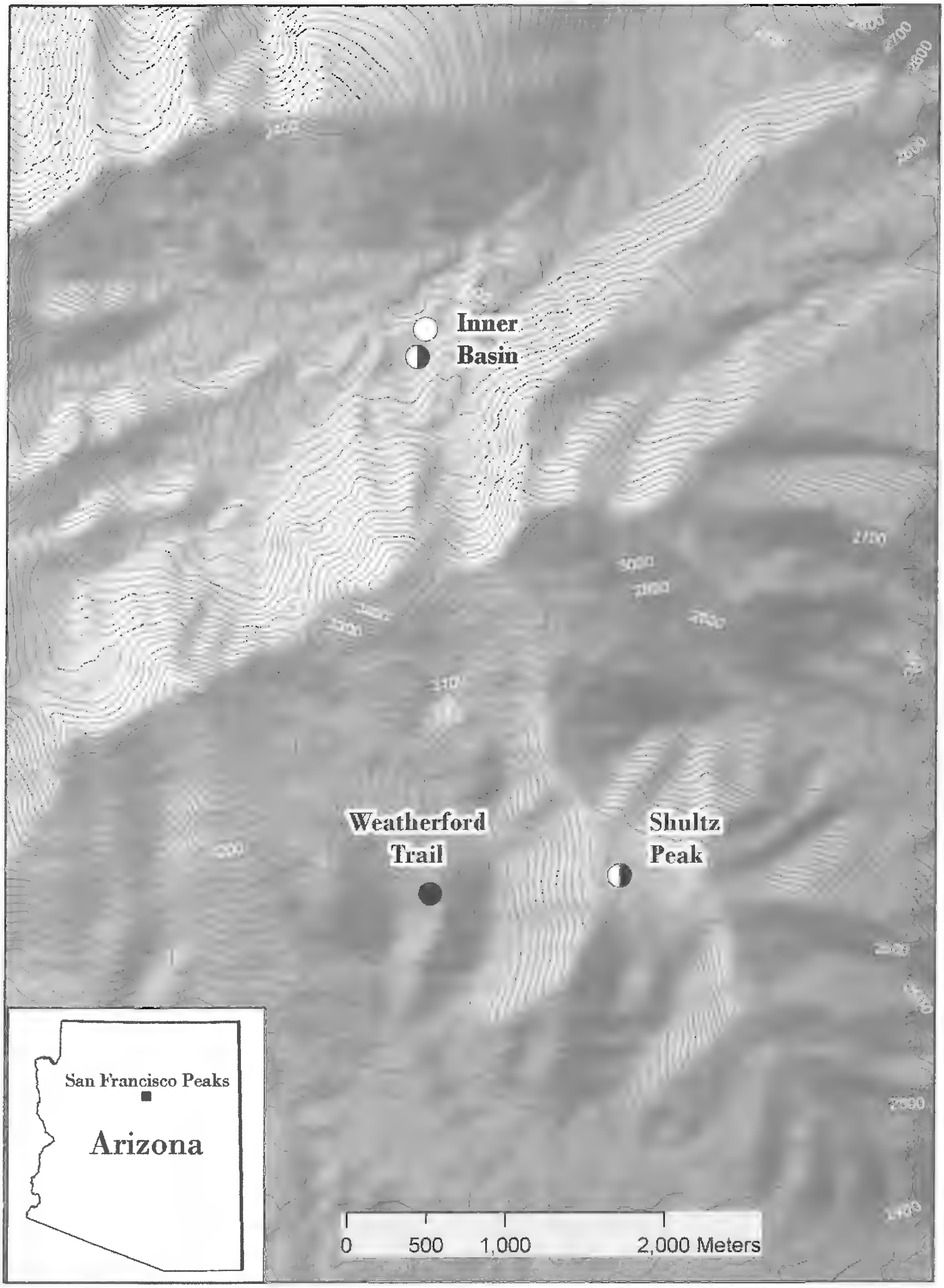

FIG. 3. The four infestations of western spruce dwarf mistletoe on the San Francisco Peaks, AZ. Dark circles indicate an infestation on bristlecone pine, white circles indicate an infestation on Engelmann spruce, half-dark and white circles indicate an infestation on both bristlecone pine and Engelmann spruce.

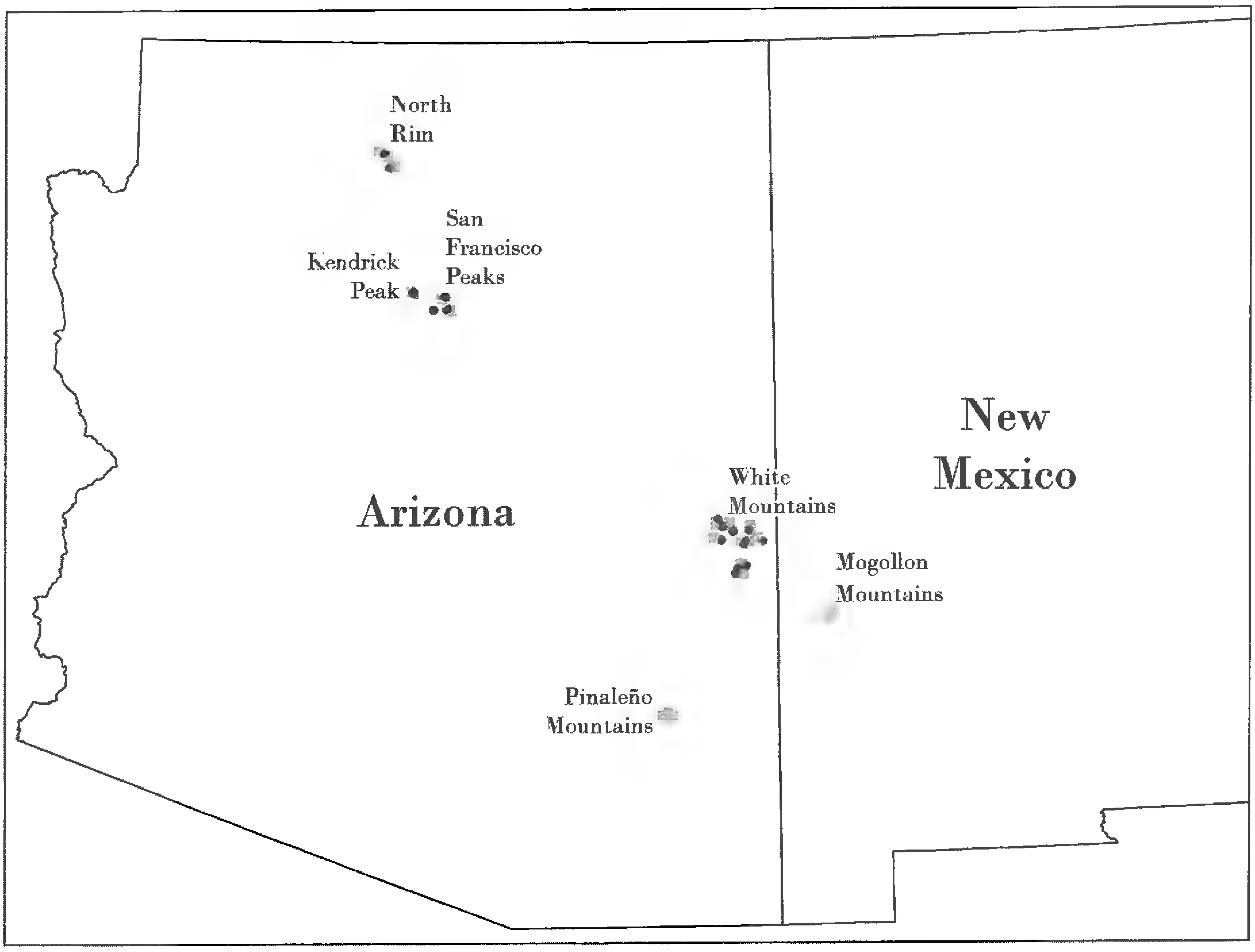

Fig. 4. Approximate locations for plant collections of western spruce dwarf mistletoe in 1975 and 1976 (gray squares) and in 2006 and 2007 (closed circles). Plants were collected from approximately the same locations for the White Mountains, San Francisco Peaks, Kendrick Peak, and the North Rim of the Grand Canyon.

other morphological characters were measured using a 10× hand lenses with a micrometer to the nearest 0.1 mm. Male plants were collected during peak anthesis and female plants were collected when fruits were mature. Over 20 male or female plants were collected for each population and morphological measurements were completed using ten randomly selected plants for each population sampled. Not all of the morphological characters that were measured in 2006–07 were measured for the 1970s data. Characters examined for both datasets included male and female plant height and basal diameter, flower diameter, perianth lobe length and width, fruit length and width, seed length and width, and plant color.

Phenology Observations.—Anthesis and seed dispersal data were recorded when plants were collected for morphological measurements in 1975, 2006, and 2007. Data for the last two years were primarily from the San Francisco Peaks and Kendrick Peak due to frequent visits to these areas. During these years, the White Mountains were only visited twice each year: once during anthesis and again during seed dispersal. Therefore, the precise times of peak anthesis and seed dispersal were estimated for the White Mountains in 2006–07. In 1975, phenology data was collected from the San Francisco Peaks, Kendrick Peak, White Mountains, and Pinaleño Mountains, Arizona.

Host Susceptibility.—In 2008, temporary 0.012 ha (radius 6 m) plots were established around 26 severely infected bristlecone pines on Schultz Peak and 13 severely infected Engelmann spruces in the Inner Basin. In each plot, all trees > 1.4 m in height were examined for dwarf mistletoe infection. For each tree, species, diameter at breast height (dbh; to the nearest cm), and a dwarf mistletoe rating (DMR, Hawksworth 1977) were

recorded. These data provided information on the relative susceptibility of bristlecone pine and Engelmann spruce to dwarf mistletoe infection on Schultz Peak and for Engelmann spruce in the Inner Basin.

Data Analysis.—Morphological data were combined from hosts on the San Francisco Peaks (bristlecone pine and Engelmann spruce) and Kendrick Peak (Engelmann spruce) and also for the White Mountains and North Rim (blue and Engelmann spruce) for analyses. Morphological data from 1975 and 1976 were included within these two data sets, but the 1970s data also included morphological measurements from the Mogollon and Pinaleño Mountains. A one-way analysis of variance (ANOVA, P-value ≤ 0.05) was used to test for significant differences between the means of each morphological character measured.

RESULTS

Morphological Data.—On average, male and female plants of western spruce dwarf mistletoe (WSDM, subsp. *microcarpum*) were larger than those of bristlecone pine dwarf mistletoe (BPDM, subsp. *aristatae*) and the differences in size were significantly different (Table 1, Appendices B–E, online). Although the largest plants we measured in 2006 and 2007 were collected from blue spruce in the White Mountains (Appendix B), the largest plants measured in the 1970s were from Engelmann spruce in the Pinaleño Mountains (Appendix E). Plant heights for the 1970s data were slightly larger than those for the 2006–07 data for BPDM, but both sets of data demonstrated that plants of WSDM were larger than BPDM. The mean basal diameter of male plants was similar, but the mean basal diameter of female WSDM plants was larger on average than female plants of BPDM and significantly different. The means for flower diameters, fruit lengths, and seed widths were significantly different, even though the differences were only about 0.1 mm or less (Table 1).

The color of male and female plants of BPDM was commonly light green or green-brown. However, many plants on the San Francisco Peaks appeared purple (Fig. 2). The color of male and female plants of WSDM was similar to BPDM, except that some plants in the White Mountains were green-blue.

Phenology.—Peak anthesis for BPDM occurred one to two weeks earlier on the San Francisco Peaks than for WSDM in the White Mountains in 2006 and 2007. Seed dispersal of BPDM also starts and ends one to two weeks earlier on the San Francisco Peaks than seed dispersal of WSDM in the White Mountains. The 1970s observations also found that BPDM flowers and disperses seed earlier than WSDM (Mathiasen & Hawksworth 1980).

Host Susceptibility.—Infection of bristlecone pine on Schultz Peak was 96% (n = 111) indicating it is a principal host of bristlecone pine dwarf mistletoe there. However, infection of Engelmann spruce was only 34% (n = 224) on Schultz Peak placing it in the occasional host class of Hawksworth and Wiens (1996). Engelmann spruce is clearly much less susceptible than bristlecone pine on Schultz Peak. However, infection of Engelmann spruce in the Inner Basin, just 5 km north of Schultz Peak, was 94% (n = 101). All of the bristlecone pines growing near severely infected Engelmann spruces in the Inner Basin were infected, but there are only about 10 bristlecone pines in the area. We also observed rare infection of limber pine (2 trees) and subalpine fir (3 trees) by BPDM on Schultz Peak.

Table 2 summarizes the principal morphological and physiological differences between BPDM and WSDM used to distinguish the two subspecies. The shoot heights, colors, and phenology, of BPDM on the San Francisco Peaks and Kendrick Peak were similar enough to group them as one population. Morphological data from Mathiasen and Hawksworth (1980) and our data demonstrated that BPDM plant heights were smaller than for WSDM populations in southern Arizona and central New Mexico. The differences in mean plant height between BPDM and WSDM were statistically significant. Additionally, color differences were found between BPDM (purple plants) and WSDM (blue-green plants). Furthermore, the periods of flowering and seed dispersal for BPDM on the San Francisco Peaks occurred one to two weeks earlier than for populations of WSDM in the White Mountains in 1975–76 and 2006–07.

Another important set of physiological/genetic characteristics that separates BPDM from WSDM are their host affinities. Bristlecone pine was the principal host of BPDM on Schultz Peak (96% infection), but we found that only 34% of the Engelmann spruce were infected there. Mathiasen and Hawksworth (1980) also

Table 1. Comparison of morphological characters of *Arceuthobium microcarpum* subsp. *aristatae* and *A. microcarpum* subsp. *microcarpum*. Data combine measurements from 1975–76 and 2006–07 for all hosts and are presented as means (ranges) [n]. Characters with an asterisk had significantly different means using ANOVA ($P \leq 0.05$). The means for seed width were rounded to the nearest 0.1 mm, but actual values were significantly different.

Character	*A. microcarpum* subsp. *aristatae*	*A. microcarpum* subsp. *microcarpum*
Plant Height (cm)		
Male*	2.7(0.8–7.0) [152]	5.6(1.8–14.9) [283]
Female*	3.6(1.4–7.0) [177]	6.4(2.0–15.7) [353]
Basal Diameter (mm)		
Male	1.8(1.0–3.0) [121]	1.9(0.8–3.4) [157]
Female*	1.8(0.6–3.0) [167]	2.0(0.8–3.8) [313]
Flower Diameter (mm)*	2.5(1.8–4.0) [287]	2.4(1.6–3.1) [266]
Fruit Length (mm)*	3.3(3.5–5.1) [281]	3.4(3.4–5.2) [440]
Fruit Width (mm)	2.1(1.7–2.9) [281]	2.2(1.9–3.1) [440]
Seed Length (mm)	2.4(1.5–3.4) [107]	2.4(1.3–3.4) [224]
Seed Width (mm)*	1.1(0.8–1.4) [107]	1.1(0.7–1.5) [244]

Table 2. Summary of the principal morphological and physiological differences between *Arceuthobium microcarpum* subsp. *aristatae* and *A. microcarpum* subsp. *microcarpum*.

Character	*A. microcarpum* subsp. *aristatae*	*A. microcarpum* subsp. *microcarpum*
Mean Plant Height (cm)		
Male Plants	2.7	5.6
Female Plants	3.6	6.4
Plant Color	Light green; green-brown; purple	Light green; green-brown; blue-green
Peak Flowering Period	One to two weeks earlier than subsp. *microcarpum*	One to two weeks later than subsp. *aristatae*
Host Susceptibility[1]		
Bristlecone pine	Principal	Unknown
Engelmann spruce	Principal/Occasional[2]	Principal
Blue spruce	Unknown	Principal
Limber pine	Rare	Unknown
Subalpine fir	Rare	Rare
Southwestern white pine	Unknown	Immune

[1]Host susceptibility classification categories are described in Hawksworth and Wiens (1996). The host susceptibility designations used for *A. microcarpum* subsp. *micorcarpum* are based on information in Hawksworth and Wiens (1996) also.

[2]Engelmann spruce was classified as a principal host for subsp. *aristatae* in the Inner Basin of the San Francisco Peaks and on Kendrick Peak, Arizona, but it was an occasional host of this mistletoe on Schultz Peak.

reported that bristlecone pine was the principal host of BPDM on Schultz Peak, and they reported a similar level of infection for Engelmann spruce (32%), but they used a different method of collecting infection data; a systematic sampling design using 27 rectangular plots. Although they classified Engelmann spruce as a secondary host of BPDM on Schultz Peak, the low incidence of infection we found indicates Engelmann spruce should be classified as an occasional host there. Based on our observations and those of Lynch (2004), blue spruce is more susceptible to infection by WSDM than Engelmann spruce, but both are principal hosts of WSDM. Because blue spruce has not been reported on Kendrick Peak or the San Francisco Peaks, we were unable to collect infection data for BPDM on this host. There is also a report of dwarf mistletoe on Chihuahua spruce (*Picea chihuahuana* Martínez) in northern Mexico by Ledig et al. (2000) which we assumed would be WSDM. However, our examination of several Chihuahua spruce populations in Chihuahua and Durango

reported to be infested with dwarf mistletoe, indicated that the spruces were infected with spruce broom rust (*Chrysomyxa arctostaphyli* Dietel) and not dwarf mistletoe. Spruce broom rust induces the formation of witches' brooms on Chihuahua spruce that are similar to those caused by dwarf mistletoes (Cibrián et al. 2007), which was undoubtedly the reason for the report of dwarf mistletoe on Chihuahua spruce in Mexico. Therefore, none of the Mexican species of *Picea* have been reported as the host of a dwarf mistletoe thus far (Hawksworth et al. 2002).

Hawksworth and Wiens (1972, 1996) defined a subspecies as geographically restricted populations having small, but consistent variations. Variations in dwarf mistletoe plant size, color, host range, and phenology have been used as the primary characteristics to identify subspecies of dwarf mistletoe (Hawksworth & Wiens 1965; Hawksworth & Wiens 1972, 1977, 1996; Hawksworth et al. 1992; Wass & Mathiasen 2003; Mathiasen 2007; Mathiasen & Daugherty 2007). Furthermore, the geographic isolation of the San Francisco Peak/Kendrick Peak BPDM populations is also consistent with Hawksworth and Wiens (1972, 1996) definition that a subspecies should be a "geographically restricted population."

ACKNOWLEDGMENTS

We thank M. Socorro González Elizondo for the Spanish translation for the Resumen. We also appreciate the field assistance of James White and Laine Smith in northern Arizona and Brian Howell in northern Mexico. Gregory M. Filip and Del Wiens provided helpful suggestions to an earlier version of the manuscript.

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BOOK REVIEW

ALHOS FARJON. 2008. **A Natural History of Conifers.** (ISBN 978-0-88192-869-3, hbk.). Timber Press, Inc., The Haseltine Building, 133 S.W. Second Avenue, Suite 450, Portland, Oregon 97204, U.S.A. (**Orders:** www.timberpress.com, 1-800-827-5622). $34.95, 304 pp., 157 color photos, 39 line drawings, 7 3/8" × 10 3/8".

A plant group that has survived 300 million years through very adverse conditions deserves a well written book. This is what we have in this volume. Mr. Farjon, retired head of the temperate section of the Kew Herbarium, is an obviously dedicated botanist and always had a working knowledge of the conifers. Upon retiring and deciding to write a book on the subject, he started to study them all over again. Here we are given an extensive study of the conifers. An enlightening chapter on corrected classification using contemporary methods tells of the many families extinct and extant which, added to DNA studies, gives a more accurate history of the group.

The ecology of the conifers and their place in history is also covered. Because these trees have been found almost all over the globe, their geography is long and involved. Of course they are also a plant of the people. Since some are fast-growing and quite dense, their connection with the construction timber industry and thus humanity is very important.

This connection segues to conifer conservation as the last area of the author's thoughts. He offers detailed information on both the unfortunate extinction of some species and the hopeful avoidance of extinction in other species.

The writing should be of interest to the non-scientist and the scientist alike. The many photographs by the author that are provided, some of which depict trees you would have to travel long, difficult ways to see for yourself, make this a wonderful book.—*Elaine Bell, Volunteer, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

A NEW CLIFF-DWELLING SPECIES OF *ZAMIA* (ZAMIACEAE) FROM BELIZE

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ABSTRACT

Zamia meermanii (Zamiaceae), a new cliff-dwelling species from Central Belize is described. It is distinguished by having 1 to 3 pendent leaves carrying coriaceous leaflets that are entire or crenulately notched on distal third, distinctly nerved on the adaxial surface, and bearing persistent tomentum on the abaxial surface. It is compared to *Zamia furfuracea* L.f. which it most closely resembles, as well as to Mesoamerican cliff-dwelling species *Zamia cremnophila* Vovides, Schutzman & Dehgan and *Zamia sandovalii* Nelson.

RESUMEN

Se describe **Zamia meermanii** (Zamiaceae), una nueva especie de Belize Central que crece en precipicios. Se puede distinguir porque tiene de 1 a 3 hojas colgantes que llevan folíolos coriáceos enteros o con muescas crenuladas en el tercio distal, con nerviación apreciable en la superficie adaxial, y tomento persistente en la superficie abaxial. Esta especie se compara con *Zamia furfuracea* L.f., la especie más semejante, y también se compara con las otras especies Mesoamericanas que también crecen en precipicios, que son *Zamia cremnophila* Vovides, Schutzman & Dehgan y *Zamia sandovalii* Nelson.

INTRODUCTION

Zamia is a New World genus ranging from the southeastern USA to Bolivia. It currently comprises 57 species (Hill et al. 2007) and is considered to be the most ecologically and morphologically diverse cycad genus (Norstog & Nicholls 1997). It includes species growing in areas with extremely high rainfall, such as *Z. roezlii* Linden from the Colombian Chocó region, and adjacent coastal Ecuador to species growing in full sun in extremely dry conditions, such as *Z. encephalartoides* Stevenson from the Santander region of Colombia. The genus also includes the only known obligately epiphytic cycad, *Z. pseudoparasitica* Yates, as well as two cliff-dwelling species: *Z. cremnophila* Vovides, Schutzman & Dehgan, and *Z. sandovalii* Nelson.

Jan Meerman, a Dutch ecologist who resides in Belize, discovered a third cliff-dwelling species of *Zamia* in February of 1999 together with Martin Meadows of the Belize Botanic Gardens during a Rapid Ecological Assessment of a private protected area. Since discovering the plant, Meerman has been collecting ecological and distribution data for this species, some of which is used in this description. He was instrumental in bringing a team from Montgomery Botanical Center to Belize to study this taxon and other Belizean Zamiaceae in August and September of 2008.

DESCRIPTION

Zamia meermanii Calonje, sp. nov. (**Figs. 1–2**). Type: BELIZE. Belize District: 60 m, 28 Aug 2008, *M. Calonje, J. Meerman & P. Griffith BZ08-152* (holotype: BRH; isotypes: FTG, MO, NY, XAL).

Species insignis habitui scopulicolus; caudex brevis, 1–3 foliis pendulis praeditus; foliola coriacea, marginibus integris vel crenulatis triente apicali, nervis distinctis adaxialibus, et paginis abaxialibus ad maturitates pubescentibus pro parte maxima secus margines.

Stems globose to cylindrical, to 27 cm long and 18 cm wide, solitary or occasionally branching on older plants. Cataphylls chartaceous, stipulate, triangular with lanceolate apex. Leaves 1–3 per stem, pendent, 42–146.5 cm long. Petiole 26–60 cm long with abruptly swollen base 2–3 cm wide, variously unarmed or carrying numerous prickles (50+) up to 3 mm tall. Rachis 50 to 109 cm long, unarmed or bearing a few prickles (< 20). Leaflets 7–23 pairs per leaf on adult plants, spaced 3–8 cm apart from each other with the point of attachment to the rachis 8.5–13.3 mm wide, obovate to oblanceolate or narrowly oblong, coriaceous, 12.5–32 cm long, 3.4–7.5 cm wide, with 31–56 veins prominently raised on adaxial surface, visible but not

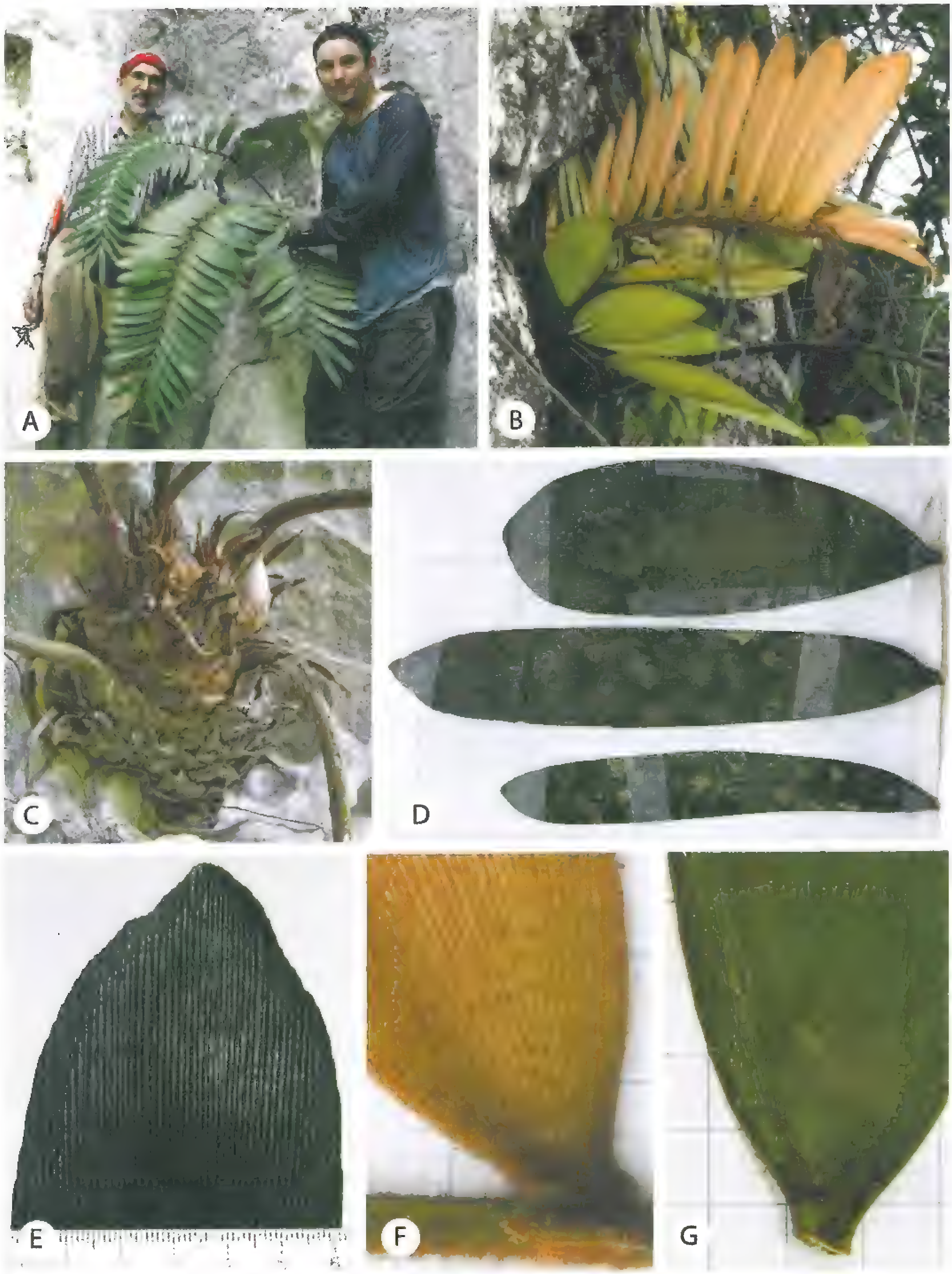

Fig. 1. (A) Habit of plant, Jan Meerman on left, Michael Calonje on right. (B) Emergent leaf showing leaf damage by *Eumaeus toxea* herbivory. (C) Detail of trunk and petioles. (D) Variation in leaflet shape. (E) Closeup of apex on adaxial surface of leaflet showing raised veins and crenulate teeth. (F) Closeup of rachis and leaflet base of immature leaf showing distinctive orange tomentum. (G) Closeup of abaxial surface near leaflet base showing persistent tomentum on adult leaf. A and C represent Calonje et al. BZ08-152; B and F represent Calonje et al. BZ08-156; D, E and G represent Calonje et al. BZ08-125.

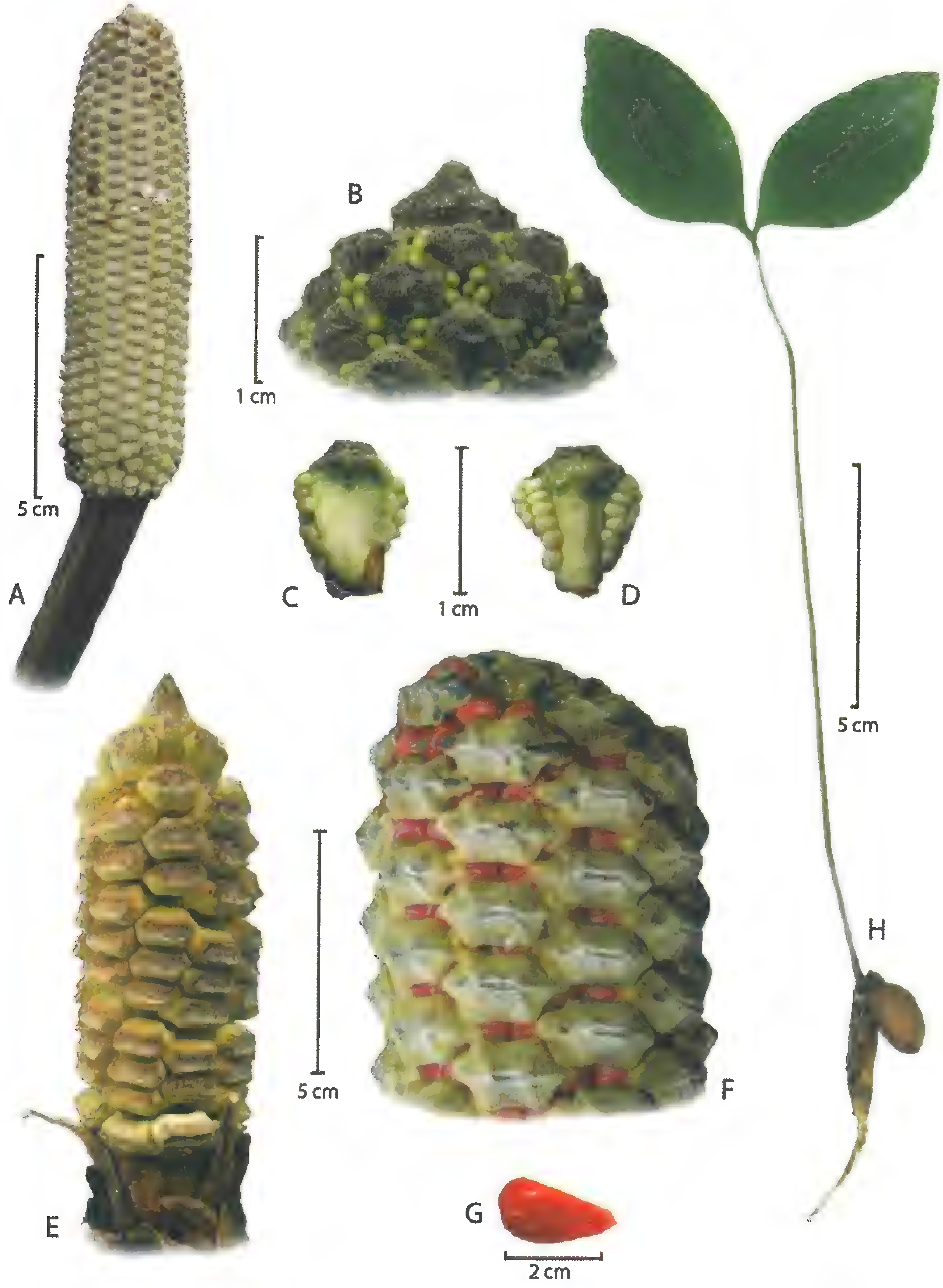

Fig. 2. (A) Immature microsporangiate strobilus. (B) Apex of microsporangiate strobilus just prior to pollen release. (C) Adaxial view of microsporophyll. (D) Adaxial view of microsporophyll. (E) Megasporangiate strobilus at receptive stage. (F) Megasporangiate strobilus at seed dehiscience. (G) Mature seed with sarcotesta. (H) Seedling with eophyll. Photographs A–E from cultivated specimens at Greenhills Botanical Collections; F and G from megasporangiate strobilus collected in habitat by Martin Meadows; H represents Calonje et al. BZ08-152.

protuberant on abaxial surface; margins entire or crenulately notched in the distal third; surface on emergent leaves reddish-brown, but densely white-tomentose, turning cream-colored with saffron-orange tomentum, and gradually maturing to green and glabrous adaxially, with some persistent brown tomentum abaxially along leaflet margins and near the point of attachment to the rachis. Eophylls typically carrying a single pair of ovate leaflets. Microsporangiate strobilus conical-cylindrical, erect, at pollen release 13–16 cm long, 2.2–2.5 cm diam., occurring individually or in groups of 2–5 or more, cream to brown colored; peduncle 9–10 cm long, 0.9–1 cm diam., covered by ferrugineous pubescence. Microsporophylls arranged in 12–18 columns, 17–30 rows; obtrullate, distal face hexagonal to oblong-hexagonal, 5.5–6 mm wide, 2.5–3 mm tall, and 1–2 mm thick ; microsporangia spheroidal, 1–1.6 mm diam., present on abaxial surface, absent on adaxial surface, 22–28 per microsporophyll arranged in two separate groups along margins. Megasporangiate strobilus cylindrical, solitary, erect at maturity, 12–20 cm long, 6–7 cm diam., tan to light-brown tomentose from emergence to maturity; peduncle 8–12 cm long, 1.5–3 cm wide, tan to brown tomentose. Megasporophylls arranged in 6–10 columns, 7–15 or more rows; distal face oblong-hexagonal, 1.5–2.2 cm wide, 1.0–1.5 cm tall, 1–1.2 cm thick, extruded to a narrow, depressed terminal facet. Seeds with sarcotesta ovoid-pyramidal, red at maturity, 2.0–2.5 cm long, 1–1.2 cm wide; sclerotesta ovoid to ovate, 1.5–1.8 cm long, 0.9–1.1 cm wide.

Other vouchers examined: **BELIZE. Belize District:** 40–70m, 25–26 Aug 2008, *M. Calonje & J. Meerman* BZ08-120 (FTG), BZ08-122 (FTG), BZ08-124 (FTG), BZ08-125 (BRH, FTG, MO, NY, XAL), BZ08-126 (FTG), *BZ08-140* (FTG), *BZ08-146* (FTG); 60 m, 28 Aug 2008, *M. Calonje, J. Meerman & P. Griffith* BZ08-154 (FTG); 70m, 27 Aug 2008, *M. Calonje, J. Meerman & P. Griffith* BZ08-156 (BRH).

Etymology.—The specific epithet honors Jan Meerman, who discovered the species.

Distribution and habitat.—Endemic to Cayo and Belize Districts in Belize, it occurs in seasonally dry tropical evergreen broad-leaved lowland forests on steep karstic hills as defined by Meerman and Sabido (2001), reaching elevations of up to 200 m. The arboreal vegetation is characterized by species such as *Comocladia guatemalensis* Donn. Sm., *Metopium brownei* (Jacq.) Urb., *Plumeria rubra* f. *acutifolia* (Poir.) Woodson, *Bursera simaruba* (L.) Sarg., *Forchhammeria trifoliata* Radlk. var. *trifoliata* , *Coussapoa oligocephala* Donn.Sm., *Caesalpinia gaumeri* Greenm., *Erythrina standleyana* Krukoff, *Pseudobombax ellipticoideum* A. Robyns, and *Thouinia paucidentata* Radlk. Disturbed open spots are characterized by the endemic *Louteridium donnell-smithii* S. Watson. These forests are semi-deciduous, with more than half of the trees being leafless for at least one month during the dry season, and with several species being leafless for four months per year. This semi-deciduous character implies that the amount of light reaching the forest floor (and under-canopy cliffs) is dramatically different between the dry and rainy seasons.

Scattered throughout these hills are vertical limestone cliffs where this species is found. It appears to be an obligate cliff-dwelling species, as it is typically found growing in cracks and crevices on sheer vertical walls and absent from the surrounding forest floor. The cliff faces are largely bare but depending on the level of weathering of the rock and the amount of shading they receive, the accompanying cliff vegetation consists largely of herbaceous plants, hemi-epiphytes and vines such as *Adiantum tenerum* Sw., *Agave angustifolia* Haw., *Anthurium schlechtendalii* Kunth subsp. *schlechtendalii*, *Anthurium verapazense* Engl., *Philodendron radiatum* Schott var. *radiatum*, *Clusia* sp., *Begonia sericoneura* Liebm., *Pitcairnia recurvata* (Scheidw.) K. Koch, *Tradescantia spathacea* Sw., *Passiflora cobanensis* Killip, and *Passiflora xiikzodz* J.M. MacDougal subsp. *xiikzodz*.

Climate.—The average annual precipitation within this species' range is estimated at 2000–2500 mm, with a distinct dry season occurring from February through May. The wettest month is July with an average monthly range of 300–440 mm, and the driest month is April with a range of 50–70 mm. The temperature ranges from 18°C to 31°C, with an annual mean temperature of 25°C. The coldest month is January and the warmest month is May. (Data derived from GIS analysis using Worldclim 1.4 climate layers as described by Hijmans et al. (2005)).

Conservation status.—The extent of occurrence for this species is estimated to be 750 sq. km as delimited by the geographic range occupied by suitable karst hills in Belize and Cayo districts. The area of occupancy, which includes only these karst formations, is 300 sq. km. Based on an average estimated population density

of 30 adult plants per km^2, the estimated total population size for this species is 9,000 plants (Meerman, unpub. data). The karst hills where this species occurs are often isolated and separated by unsuitable habitats such as lowland forest, lowland savannas, and agricultural areas. In addition, this species occurs in discrete populations of only a few individuals, and does not appear to occur on all suitable habitats within its geographic range. As a result of the isolation between karst mountains and the clumped distribution of this species, populations are considerably fragmented. Visits to 12 different localities where this species occurs appear to indicate that reproduction is occurring and seedling regeneration is healthy.

The primary threat to this species appears to be fire, utilized in adjoining areas for slash and burn agriculture. These fires have been observed spreading up surrounding karst hills and decimating native vegetation. Another important threat to this species is mining for construction aggregates and dolomite, with several active and planned quarries in the region. Recent fieldwork in Belize suggests that illegal wild collection of cycad plants and seeds has occurred in the past and may present an additional threat to this species. Hopefully, the difficult terrain and inaccessibility of this cliff dwelling plant, combined with the fact that approximately 50% of its area of occupancy lies within protected areas will help minimize the risk of illegal harvesting. Specific locality information has been purposefully withheld in order to further minimize this risk.

Due to its limited extent of occurrence and area of occupancy, the fragmented nature of its populations, and the threats caused by fire, mining, and illegal harvesting, this species should be listed as Endangered (EN) based on IUCN Red List criteria ab(i–iv) and 2ab(i–iv) (IUCN, 2001).

Reproductive phenology.—Elongating microsporangiate strobili have been observed in August and September in habitat, and pollen releasing strobili have been observed in October and November under cultivation at Green Hills Botanical Collections near San Ignacio. A single mature megasporangiate strobilus, with about a third of the seeds already dehisced, was collected in September of 2006, and another, totally dehisced with most seeds cleaned of sarcotesta, was collected in January 19 of 2006 by Martin Meadows of Belize Botanic Gardens. During the course of fieldwork with this species in August of 2008 our team found several distinct groupings of seedlings with newly-emerged eophylls, indicating that megasporangiate strobili probably disintegrated two to three months earlier. Further work is required to better understand the reproductive phenology of this species.

Ecology.—A large number of young seedlings observed during the course of fieldwork indicate that reproduction is healthy and the pollinating agent is active, although it has not yet been observed. Seedlings germinating on the forest floor suffer 100% mortality within a year or two, suggesting the forest floor habitat is unsuitable for this species (J. Meerman, pers. comm.). In August of 2008 our team observed a female plant with its peduncle attached and several seedlings growing directly underneath on the forest floor. Several of these seedlings from this same strobilus had also germinated in a fissure on the cliff directly above the mother plant, indicating that some unknown dispersal agent had moved individual seeds or a piece of the strobilus to this location. Larvae of *Eumaeus toxea* Godart butterflies were observed feeding on emergent leaves.

DISCUSSION

Zamia meermanii is most similar in appearance to *Zamia furfuracea* L.f. from southeastern Veracruz, Mexico. Both species have obovate to oblanceloate or narrowly oblong coriaceous leaflets with persistent tomentum on the abaxial side of leaflets, distinct veins on the adaxial side of leaflets, and a similar number of maximum leaflet pairs per leaf (ca. 25). *Zamia meermanii* differs from *Zamia furfuracea* in having usually solitary stems as opposed to freely branching stems; holding 1–3 pendent leaves per crown, rather than 5–7 erect or slightly arching leaves per crown; eophylls with a single pair of leaflets rather than eophylls with two pairs of leaflets, leaves cream-colored and covered with saffron-orange tomentum just prior to maturing as opposed to light green with predominantly white tomentum prior to maturing; coriaceous leaflets to 0.8 mm thick compared to coriaceous or extremely coriaceous leaflets to 1 mm thick; leaflet length to 28

TABLE 1. Diagnostic reproductive characters for *Zamia furfuracea* and cliff-dwelling *Zamia* species.

	Zamia meermanii	***Zamia cremnophila***	***Zamia sandovalii***	***Zamia furfuracea***
Microsporangia per microsporophyll	22–28	14–18	14–18	40–42
Microsporangia diameter (mm)	1–1.6	0.65–0.78	0.6	0.8–1.2
Microsporangiate strobilus peduncle length (cm)	9–10	2.5–3	6.7	8–10
Megasporangiate strobilus length (cm)	12–20	8.5–14	9–17	10–24
Megasporophyll rows	7–15	4–8	4–7	4–15
Megasporophyll width (cm)	1.5–2.2	1.6–2.6	2.5–3.5	1.5–1.8
Megasporantiate strobilus peduncle length (cm)	8–12	4–5	3.6–6	10–20
Sclerotesta length (mm)	1.5–1.8	1.5–1.7	1.8–2.2	1.1–1.5

Data derived from measurements by author, Whitelock 2002, Nelson 2006, and Schutzman et. al. 1988.

cm compared to 18 cm; protuberantly raised veins on adaxial surface to 1.5 mm wide rather than slightly raised, narrower veins to 0.8 mm wide; and 22–28 microsporangia on abaxial side of microsporophylls as opposed to 40 or more on *Z. furfuracea*.

Zamia meermanii shares this unusual cliff-dwelling habit with two other Mesoamerican *Zamia* species: *Zamia cremnophila* from Mexico and *Zamia sandovalii* from Honduras. All three species typically carry 1–3 pendent leaves. *Zamia meermanii* is easily differentiated from the two other species by leaflet features alone (see key below).

1. Leaflets with distincly raised veins on adaxial surface and persistent tomentum on abaxial surface ______ **Z. meermanii**
1. Leaflets plane, without distinctly raised veins on adaxial surface and without persistent tomentum on abaxial surface.
   2. Adaxial surface of petiole with distinct longitudinal groove ______ **Z. cremnophila**
   2. Adaxial surface of petiole rounded, without longitudinal groove ______ **Z. sandovalii**

It has distinctly raised veins on the adaxial surface, persistent tomentum on the abaxial surface, and margins that are entire or crenulately notched in the upper third, whereas *Z. sandovalii* and *Z. cremnophila* both have plane leaflets with no distinct raised veins on the adaxial surface, are glabrous on the adaxial surface, and have margins that are distinctly toothed on the distal half. *Zamia sandovalii* median leaflets are strongly falcate as opposed to those of *Z. meermanii* and *Z. cremnophila*, which are typically straight. *Zamia meermanii* and *Z. cremnophila* eophylls typically possess two leaflets, whereas *Z. sandovalii* eophylls typically possess four leaflets.

In addition to the vegetative characters that easily distinguish these three species, reproductive characters are also useful (Table 1). *Zamia meermanii* microstrobili have longer peduncles and possess more and larger microsporangia per microsporophyll than Z. *cremnophila* and Z. *sandovalii*. Megastrobili of Z. *meermanii* can be longer and with more sporophyll rows and have longer peduncles than either *Z. cremnophila* or *Z. sandovalii*. Seeds of *Z. sandovalii* are the largest of the group, and those of *Z. meermanii* and *Z. cremnophila* are of a similar smaller size. Until a well-resolved phylogeny of *Zamia* is available, we have no way to determine if the cliff-dwelling habit evolved more than once in the genus.

ACKNOWLEDGMENTS

Funding in support of the 2008 Belize expedition which resulted in the description of this species was generously provided by the Association of Zoological Horticulture (AZH), Tim Gregory, and Montgomery Botanical Center (MBC). Jan Meerman of Biodiversity & Environmental Resource Data Systems of Belize introduced me to this species and participated in all fieldwork. Patrick Griffith (MBC) assisted in data and

specimen collection, and editing the manuscript. Green Hills Botanical Collections donated significant in-kind support by providing lodging, equipment and work infrastructure in Belize. Belize Botanic Gardens provided megasporangiate strobilus images and phenological data. Alan Meerow and Bart Schutzman provided assistance with the Latin diagnosis and comments on the manuscript. Alberto Taylor (PMA), Anders Lindstrom of Nong Nooch Tropical Botanic Garden, Miguel Angel Pérez-Farrera (HEM), and Chad Husby (MBC) provided comments on the manuscript. The Belize Forest Department granted the scientific research and collecting permit (CD/60/3/08(45)) supporting research on Belizean Zamiaceae, as well as herbarium infrastructure for preservation of voucher specimens.

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BOOK REVIEW

Lynne Chapman, Noelene Drage, Di Durston, Jenny Jones, Hillary Merrifield, and Billy West. 2008. **Tea Roses: Old Roses for a Warm Climate.** (ISBN 9781877058677, hbk.). Rosenberg Publishing Pty Ltd, P.O. Box 6125, Dural Delivery Centre, New South Wales 2158, Australia. (**Orders:** www.rosenbergpub.com.au, 61-2-9654-1502, 61-2-9654-1338 fax). $59.95, 240 pp., color photographs, glossary, appendices, bibliography, index, 9 1/4" × 11 1/4".

This beautiful book is presented by six ladies who love roses with a passion and realized the lack of true history of the tea rose in Australia. The tea rose or Tea-Scented China rose was hidden in China for centuries. They were brought to Europe in about 1820 and later to Australia. They have been planted, studied, and hybridized through the years, losing and gaining favor over and over again.

With over two hundred pages covering every aspect of the tea rose, this book is a scientific work and just fascinating for a rose lover. The roses are discussed in detail, from the horticultural and botanical facts to the unique history. Sixty-five teas are presented in all, each with a list of distinguishing features, cultivation background, location, and the most gorgeous photos. The photography is quite fantastic and is mostly provided by the authors as both beautiful floral close-ups and broader plant views. Pictures of paintings and other printed recordings of the roses round out the visuals of this carefully crafted work.

Of additional note is the authors' account of current studies to distinguish true descendents from mere family extensions. Tea rose "imposters" are discussed and a "What not to grow" list from 1922 is given.

A book for the beauty of the rose and a book for the factual study of the rose, *Tea Roses* should strike a chord with a variety of readers.—*Elaine Bell, Volunteer, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

A NEW SPECIES OF *ZAMIA* (ZAMIACEAE) FROM THE MAYA MOUNTAINS OF BELIZE

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ABSTRACT

Zamia decumbens (Zamiaceae), a new species from the Maya Mountains of Belize, is described and illustrated. It has affinity with *Zamia tuerckheimii*, *Zamia bussellii/onan-reyesii*, and *Z. monticola*, to which it is compared.

RESUMEN

Se describe ilustra **Zamia decumbens** (Zamiaceae), una especie nueva de las montañas Maya de Belize. Muestra afinidades con *Zamia tuerckheimii*, *Zamia bussellii/onan-reyesii*, y *Z. monticola*, con las que se compara.

INTRODUCTION

In December of 1997, while conducting research on wild nutmeg trees, John Janovec and Amanda Neill were led to the bottom of a large sinkhole in the Maya Mountains of Belize by naturalist guide Valentino Tzub to look at an interesting group of plants he called "corn palms." At the bottom of the sinkhole, they found an old Mayan kiln and many pottery shards, and a dense population of *Zamia* (Janovec & Neill 2003). The plants did not match the description of any *Zamia* known from Belize at the time, but shortly after their return, Dr. Dennis Stevenson of the New York Botanical Garden informed them that the holotype of *Zamia prasina* Bull, a species described in 1881 (Bull 1881), had recently been re-discovered at the Kew herbarium. Janovec and Neill (2003) wrote that they connected these specimens to the sinkhole plants, and the name *Zamia prasina* has since been applied to this plant in the horticultural trade and several publications (see Balick 2000; Whitelock 2002).

In August, 2008, Montgomery Botanical Center (MBC) sponsored an expedition to Belize to shed some light on this poorly-known species and other Belizean Zamiaceae. During the course of the expedition, it became clear that the leaflets of these sinkhole-dwelling plants, which were chartaceous, gradually acuminate, with a distinctly raised longitudinal fold, and margins that are entire or with a few minute teeth at the apex, were very different from the leaflets of the *Z. prasina* holotype, which were coriaceous, abruptly acuminate, strongly serrulate and lacking a longitudinal crease. We determined that *Z. prasina* was in fact a prior valid name for *Z. polymorpha* D.W. Stev., A. Moretti & Vázq. Torres (see Calonje et al., pages 43 – 49, this volume), and that the cycads found in the sinkhole belonged to an undescribed species.

During the cycad research expedition, the authors studied four separate populations of this species in Belize, gathering enough data to formally describe it.

SPECIES DESCRIPTION

Zamia decumbens Calonje, Meerman, M.P. Griff. & Hoese, sp. nov. (**Figs. 1–3**). TYPE: BELIZE. TOLEDO DISTRICT: bottom of sinkhole, 350–400 m, 2 Sep 2008, *M. Calonje, J. Meerman & P. Griffith BZ08-201* (HOLOTYPE: BRH; ISOTYPES: FTG, MO, NY, XAL).

Species *Z. tuerckheimii* Donn.Sm. affinis sed caule decumbente et pedunculo pollinis longissimo.

Fig. 1. Habit and habitat of *Z. decumbens*. A. Adult female plant with naturalist guide Valentino Tzub. B. View from sinkhole bottom at type locality of *Z. decumbens*.

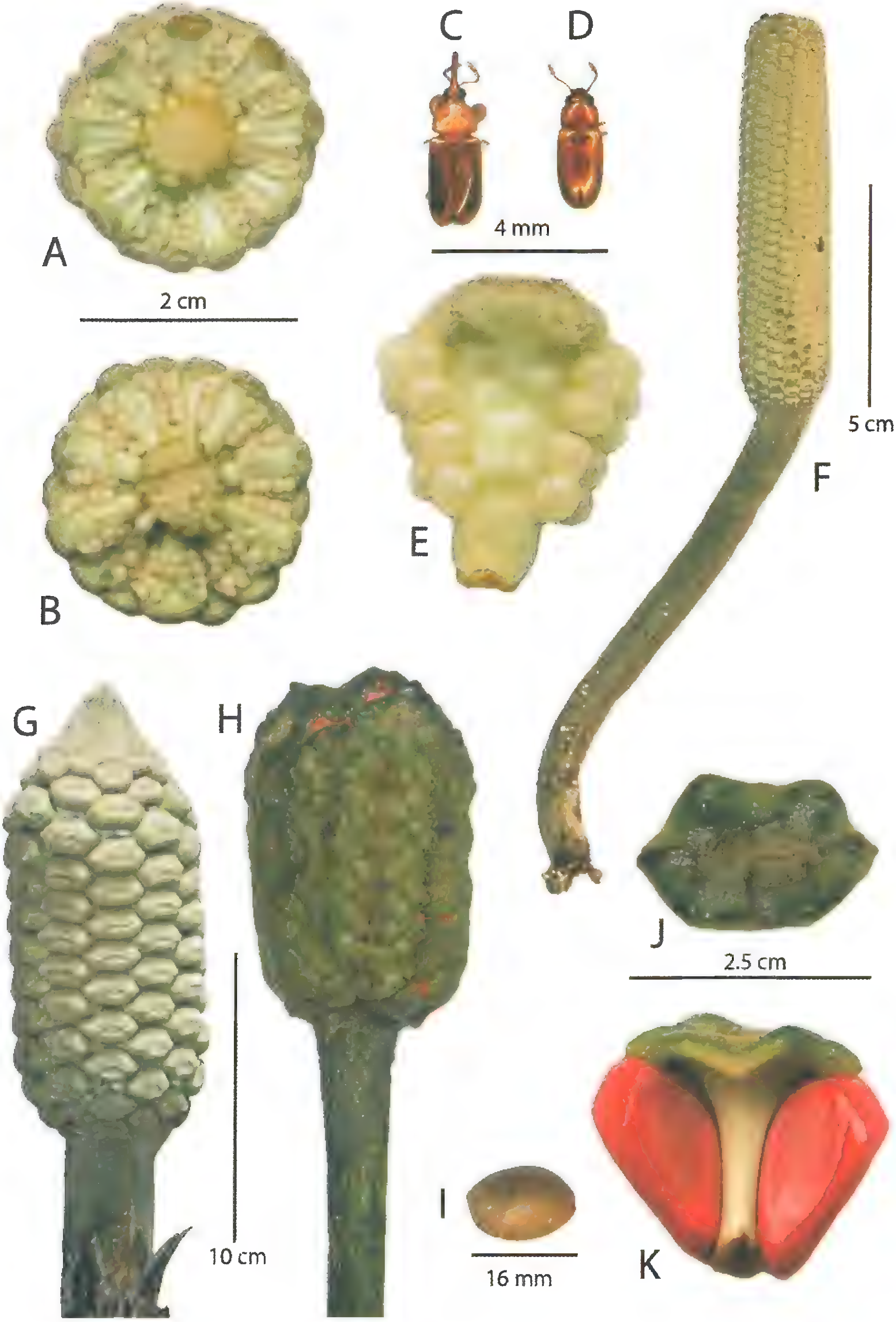

Fig. 2. Reproductive features of *Z. decumbens*. All photographs derived from type locality population. A. Cross section of microsporangiate strobilus, adaxial side. B. Cross section of microsporangiate strobilus, abaxial side. C. *Rhopalotria sp*., putative pollinator of *Z. decumbens*. D. *Pharaxonotha sp*., putative pollinator of *Z. decumbens*. E. Microsporophyll, abaxial side. F. Microsporangiate strobilus. G. Megasporangiate strobilus at pollen receptivity stage. H. Mature megasporangiate strobilus. I. Seed with sarcotesta removed. J. Megasporophyll face. K. Megasporophyll with mature seed, abaxial side.

Stems globose to cylindrical, to 80 cm long and 6.7–11 cm wide, decumbent and occasionally branching on older plants, in habitat often rotting at base and rooting adventitiously from along the horizontal stems. Vegetative cataphylls tan-tomentose, chartaceous, stipulate, shallowly triangular to triangular with short, brown apex; strobilar cataphylls tan-tomentose, chartaceous, narrowly triangular with elongated light-tan lanceolate apex. Leaves on adult plants 5–17 per crown, erect or arching, 90–175 cm long, light green when emerging, turning dark green when mature. Petiole 30–55 cm long with abruptly swollen base 2.2–3.2 cm wide, moderately to heavily armed with prickles up to 5.3 mm long. Rachis 60–120 cm long, unarmed or sparsely armed in the proximal third. Leaflets to 28 pairs per leaf, 2.8–4.1 cm wide, 17.5–29 cm long, spaced 2–5.5 cm apart from each other with the point of attachment to the rachis 4.5–6 mm wide, chartaceous, lanceolate with gradually tapering apex and distinct longitudinal furrow, straight or slightly falcate, margins entire or with a few teeth restricted to apex. Eophylls typically with a single pair of ovate leaflets. Microsporangiate strobilus conical-cylindrical, emerging erect with peduncles progressively leaning outward horizontally, at pollen release 10–16.5 cm long, 2.1–2.5 cm diam., occurring individually or in groups of 2–6 or more, cream to brown; peduncle 12–23 cm long, 0.9–1 cm diam., green with brown pubescence. Microsporophylls arranged in 16–18 columns, 26–36 rows; obtrullate, distal face hexagonal to oblong-hexagonal, 3.0–3.5 mm wide, 4.0–4.5 mm tall; microsporangia spheroidal, 1–1.2 mm diam., present on abaxial surface, absent on adaxial surface, 12–18 per microsporophyll arranged in two separate groups along margins. Megasporangiate strobilus cylindrical, solitary, erect at maturity, 12–20 cm long, 5.7–6.4 cm diam., emerging cream-colored tomentose and maturing to glabrous light or dark green with patches of tan tomentum remaining on inner facet and margins of megasporophylls; peduncle 7–13 cm long, 1.5–2 cm wide, green to brown tomentose. Megasporophylls arranged in 8–12 columns, 4–16 rows; distal face hexagonal to oblong-hexagonal, 2.25–2.9 cm wide, 1.6–1.8 cm tall, 2.5–4 mm thick, with a depressed terminal facet 9.5–12mm wide, 3.5–4.55 tall. Seeds with sarcotesta ovoid to ovoid-pyramidal, red at maturity, 1.7–2.0 cm long, 1.1–1.45 cm wide; sclerotesta ovoid to ovate, 1.45–1.65 cm long, 1.05–1.43 cm wide.

Other vouchers examined: **BELIZE. Cayo District:** 170–200 m, 19 Aug 2008, *M. Calonje, J. Meerman, M.A. Perez-Farrera, B. Arevalo BZ08-040* (FTG), *BZ08-041* (FTG), *BZ08-053* (BRH). **Toledo District:** 100–200 m, 9,11,12 Mar 1987, *Davidse & Brant 32232* (MO); bottom of sinkhole, 700 m, 3 Oct 1999, *Janovec & Neill 1185, 1186* (FTG). bottom of sinkhole, 300–320m, 1 Sep 2008, *M. Calonje & P. Griffith BZ08-180* (FTG), *BZ08-189* (FTG), *BZ08-194* (FTG); bottom of sinkhole, Toledo District, 700 m, 2 Sep 2008, *M. Calonje, P. Griffith, J. Meerman, & V. Tzub BZ08-222* (FTG), *BZ08-224* (FTG), *BZ08-225* (FTG), *BZ08-227* (FTG), *BZ08-231*(BRH), *BZ08-232* (FTG); 350–400m, 2 Sep 2008, *M. Calonje, J. Meerman & P. Griffith BZ08-180* (FTG), *BZ08-189* (FTG), *BZ08-194* (FTG), *BZ08-202* (FTG).

Etymology.—The specific epithet refers to the decumbent habit of the stems.

Distribution and habitat.—Known from several locations in the Maya Mountains of Belize in Toledo, Cayo, and Stann Creek districts at elevations of 150–700 m. Currently considered a Belizean endemic, but some populations occur near the border with Guatemala, and since the Maya Mountains extend into Southeastern Petén Province, it is likely to occur here as well. These locations were within Tropical Evergreen Broadleaf Lowland Forest variants as defined by Meerman and Sabido (2001) and over a number of geological formations, most notably late Cretaceous limestones, but also older Triassic metamorphic bedrock to a lesser extent (Cornec 2003).

The authors have observed seven different occurrences of this species found throughout the Maya Mountains of Belize, encompassing an area of approximately 2600 km^2. However, each of these populations was extremely small and restricted to rocky mountaintops and ridges or on the bottom of sinkholes. The largest populations found have been inside two steep-walled sinkholes in Toledo district, each approximately 50–80 m wide and 30–60 m in depth, with approximately 150 large plants of reproductive age. The mountaintop and ridge populations observed to date have been much smaller, with a maximum of 20 plants observed, all much smaller in size than those observed in the sinkholes. The factor limiting the distribution of this species appears to be reduced soil moisture. In the sinkholes, the plants are found growing near the sinkhole walls within the sinkhole overhang drip line, where there is less light and they are protected from direct rainfall. Few other plant species are present in these areas, in low densities, with large areas of unoccupied soil (Table 1). The mountaintop populations may benefit from the quick-draining substrate provided by

Table 1. Associated vegetation observed within dry area of sinkhole in the type locality for *Zamia decumbens*.

Taxon	**Family**
Justicia sp.	Acanthaceae
Louteridium donnell-smithii	Acanthaceae
Adiantum macrophyllum	Adiantaceae
Syngonium podophyllum	Araceae
Chamaedorea geonomiformis	Arecaceae
Aristolochia veracruzana	Aristolochiaceae
Forchhammeria trifoliata var. *trifoliata*	Capparidaceae
Tradescantia spathacea	Commelinaceae
Dracaena americana	Dracaenaceae
Acalypha macrostachya	Euphorbiaceae
Episcia punctata	Gesneriaceae
Calatola laevigata	Icacinaceae
Dorstenia lindeniana	Moraceae
Ficus sp.	Moraceae
Passiflora lancetillensis	Passifloraceae
Peperomia sp.	Piperaceae
Piper spp.	Piperaceae
Deherainia smaragdina var. *smaragdina*	Theophrastaceae
Myriocarpa heterostachya	Urticaceae
Myriocarpa longipes	Urticaceae
Urera baccifera	Urticaceae

the rocky environment. In Toledo district, other lithophytic species such as *Chamaedorea adscendens* and *Chamaedorea schippii* were also observed growing in the same environment.

Climate—The average annual precipitation within this species' range is estimated at 1800–2800 mm, with a distinct dry season occurring from February through May. The wettest month is July, with an average monthly range of 205–580 mm; the driest month is April, with a range of 50–70 mm. The temperature ranges from 16–31°C, with an annual mean temperature of 22–25°C. The coldest month is January and the warmest month is May (data derived from GIS analysis using Worldclim 1.4 climate layers as described by Hijmans et al. (2005)).

Reproductive phenology.—The reproductive phenology of this little-studied species is not well known and no distinct periodicity is evident based on the authors' visits in September of 2008, as well as the examination of photographic evidence archived at Montgomery Botanical Center from John Janovec and Amanda Neill's visits to the sinkhole populations in August of 1999, and June of 2001. Immature, pollen-releasing, and old microsporangiate strobili were observed during all three visits. Receptive megasporangiate strobili were observed in August and September, and near-mature strobili were observed in June and September.

Ecology.—Several microsporangiate strobili at pollen-release stage observed at both sinkhole localities harbored numerous snout weevils of an unknown *Rhopalotria* species, as well as clavicorn beetles of an unknown *Pharaxonotha* species (Fig. 2c, d). Both genera are believed to be pollinators of *Zamia* and have previously been found in microsporangiate strobili of *Zamia furfuracea* L.f. (Vovides 1991) and *Z. pumila* L. (Tang 1987), as well as entering and exiting both microsporangiate and megasporangiate strobili in many natural *Zamia* populations in Panama (Alberto Taylor, pers. comm.). A preliminary examination of the *Rhopalotria* insects suggests that they are either conspecific or close relatives to *Rhopalotria mollis*, one of the known pollinators of *Zamia furfuracea* L.f. (William Tang, pers. comm.).

Ceratozamia robusta Miq. occurs throughout the range of *Z. decumbens* and both species were observed growing sympatrically at one location in Northern Cayo district. *Zamia decumbens* was also observed growing together with *Zamia variegata* Warsz. at one location in southern Toledo district, with no evidence of hybridization. These two species are unlikely to overlap much geographically, as most observed populations of *Z. decumbens* occur above 300 m, which is the maximum of the altitudinal range of *Z. variegata*.

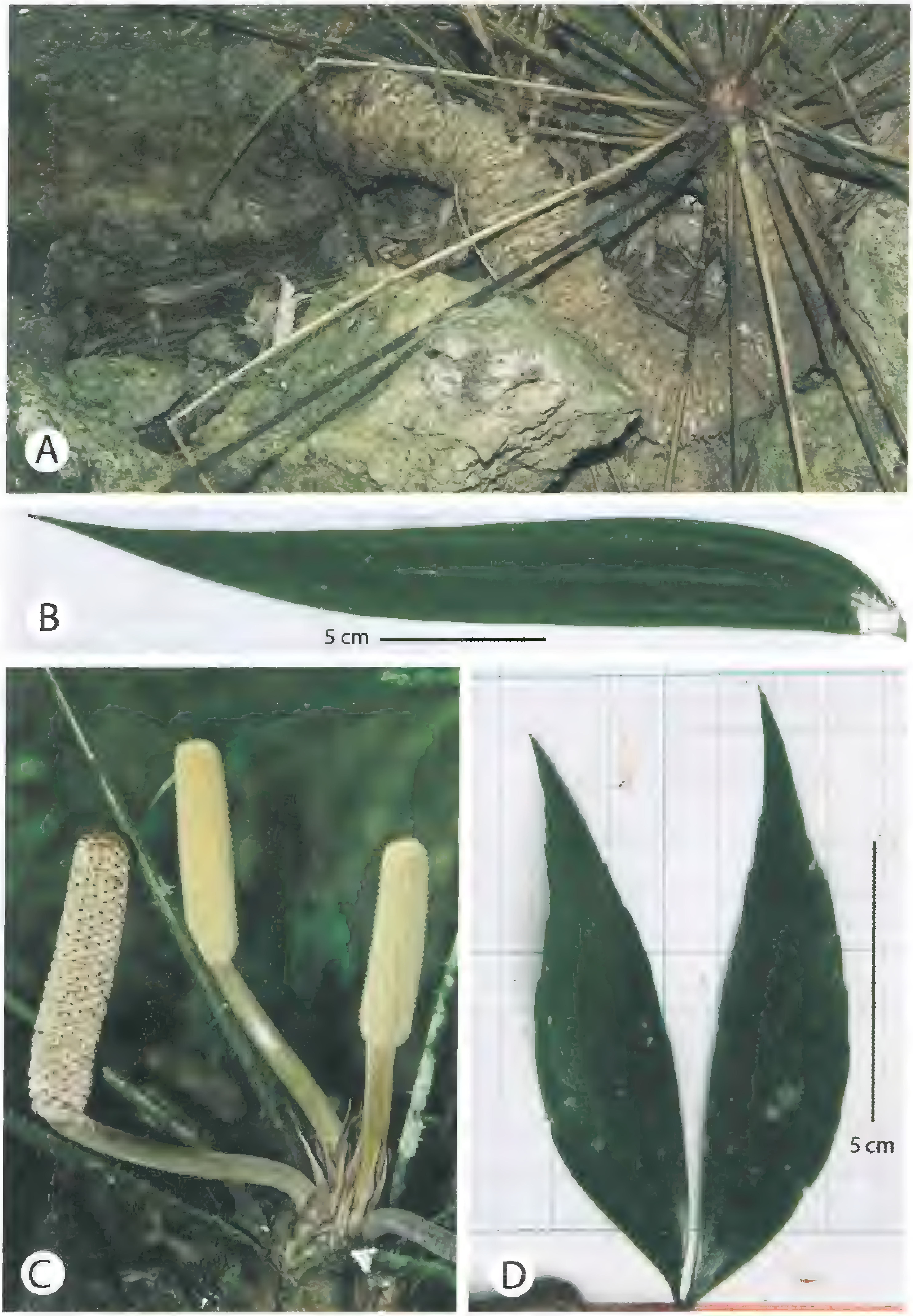

Fig. 3. Diagnostic characters of *Z. decumbens*. All photographs derived from type locality population. A. Decumbent stem with rotted base. Notice decomposition stain on rock behind. B. Typical median leaflet. C. Long-pedunculate leaning microsporangiate strobili. D. Eophylls.

DISCUSSION

Zamia decumbens appears to be most closely related to *Zamia tuerckheimii* Donn.Sm. from Guatemala as well as a new species described from Honduras. The taxonomic priority for this Honduran species, described separately as *Zamia bussellii* Schutzman, R.S. Adams, J.L. Haynes & Whitelock and *Z. onan-reyesii* C. Nelson & Sandoval is currently in dispute and will therefore be treated here as *Z. bussellii/onan-reyesii.*

Zamia decumbens differs from both species in having decumbent stems to 80 cm long that often rot at the base and re-root horizontally. *Zamia tuerckheimii* has erect or leaning stems to 3 m tall, and *Z. bussellii/onan-reyesii* has erect or leaning stems to 2 meters tall. All three species have leaflets with a marked longitudinal crease most prominent near the point of attachment to the rachis, but the leaflets of *Z. bussellii/onan-reyesii* are characteristic enough to distinguish it vegetatively from the two other species (Fig. 4). *Zamia bussellii/onan-reyesii* leaflets are papyraceous and with prominent teeth on the lower margin compared to those of the other two species, which are chartaceous with margins entire or minutely toothed at the apex. Leaflets of *Z. decumbens*, measuring 2.8–4.1 cm in width, are typically narrower than those of *Z. tuerckheimii*, which typically measure 4–9 cm in width. Another useful vegetative distinction between the two species is that *Z. decumbens* has moderately to heavily armed petioles whereas those of *Z. tuerckheimii* are unarmed or sparsely armed.

Mature microsporangiate strobili of *Zamia decumbens* are easily distinguished from those of the two other species as they have long peduncles 11–23 cm in length causing them to lean outward, whereas *Z. tuerckheimii* has erect to slightly leaning strobili with peduncles to 6.5 cm long and *Z. bussellii/onan-reyesii* has erect to slightly leaning strobili with peduncles to 8.5 cm long. *Zamia bussellii/onan-reyesii* has the largest microsporangiate strobili, measuring up to 27.5 cm long and 3.8 cm in diameter, whereas those of *Z. tuerckheimii* measure 14–17 cm in length and 2.5 to 4 cm in diameter, and those of *Z. decumbens* measure 10–16.5 cm. *Zamia bussellii/onan-reyesii* is further differentiated from the other two species because it has more than 40 microsporangia arranged in a single group on the abaxial surface of the microsporophyll whereas *Z. decumbens* has 12–18 microsporangia arranged in two separate groups and *Z. tuerckheimii* has 18–26 microsporangia arranged in two separate groups. The microsporophylls of *Z. tuerckheimii* are elongate triangular, approximately 1.8–2.5 times as long as they are wide, whereas those of *Z. decumbens* and *Z. bussellii/onan-reyesii* are roughly triangular and approximately 1.3 to 1.5 times as long as they are wide.

The megasporangiate strobili of *Z. bussellii/onan-reyesii* are the largest of the group, measuring 22.4–25.2 cm tall and 10–11.2 cm wide with sporophylls faces 4.5–5 cm tall and 4.3–4.6 cm wide, compared to those of *Z. tuerckheimii* which are 16.3–22 cm tall and 8.3–10 cm wide with sporophyll faces 1.8–2.2 cm tall and 2.3–3.8 cm wide, and to those of *Z. decumbens* which are 12–20 cm tall and 5.7–6.4 cm wide with sporophyll faces 1.6–1.8 cm tall and 2.25–2.9 cm wide. See the following dichotomous key and Table 2 for summary of diagnostic characters. The known geographical ranges of the three species do not overlap (Fig. 5).

KEY TO *Z. BUSSELLII/ONAN-REYESII*, *Z. DECUMBENS*, *Z. TUERCKHEIMII*

1. Leaflets papyraceous with prominent teeth on lower margin ________ **Z. bussellii/onan-reyesii**
1. Leaflets chartaceous with entire margins or minutely toothed at the apex.
   2. Stem decumbent, microsporangiate strobili peduncle 11–23 cm long ________ **Z. decumbens**
   2. Stem erect or leaning, microsporangiate strobili peduncle to 6.5 cm long ________ **Z. tuerckheimii**

One other species, *Zamia monticola* Chamb. appears to share some similarities with *Z. decumbens* in leaf length, leaflet shape and size, and microsporangiate strobilus size. It was described by Charles J. Chamberlain based on a single male plant cultivated from seed reportedly collected near Naolinco Crater in the vicinity of Xalapa, Mexico. Chamberlain (1926) contends that the single plant sprouted from a batch of seeds thought to be *Ceratozamia mexicana*. The species has never been found again in the area where it was reportedly collected, and it is thought that it is either extinct, or that Chamberlain's seeds became mixed in his glasshouse and this species was acquired elsewhere (Hill 2004). Material collected in southern Alta Verapaz in Guatemala is currently being identified as this species, but this Guatemalan material is poorly

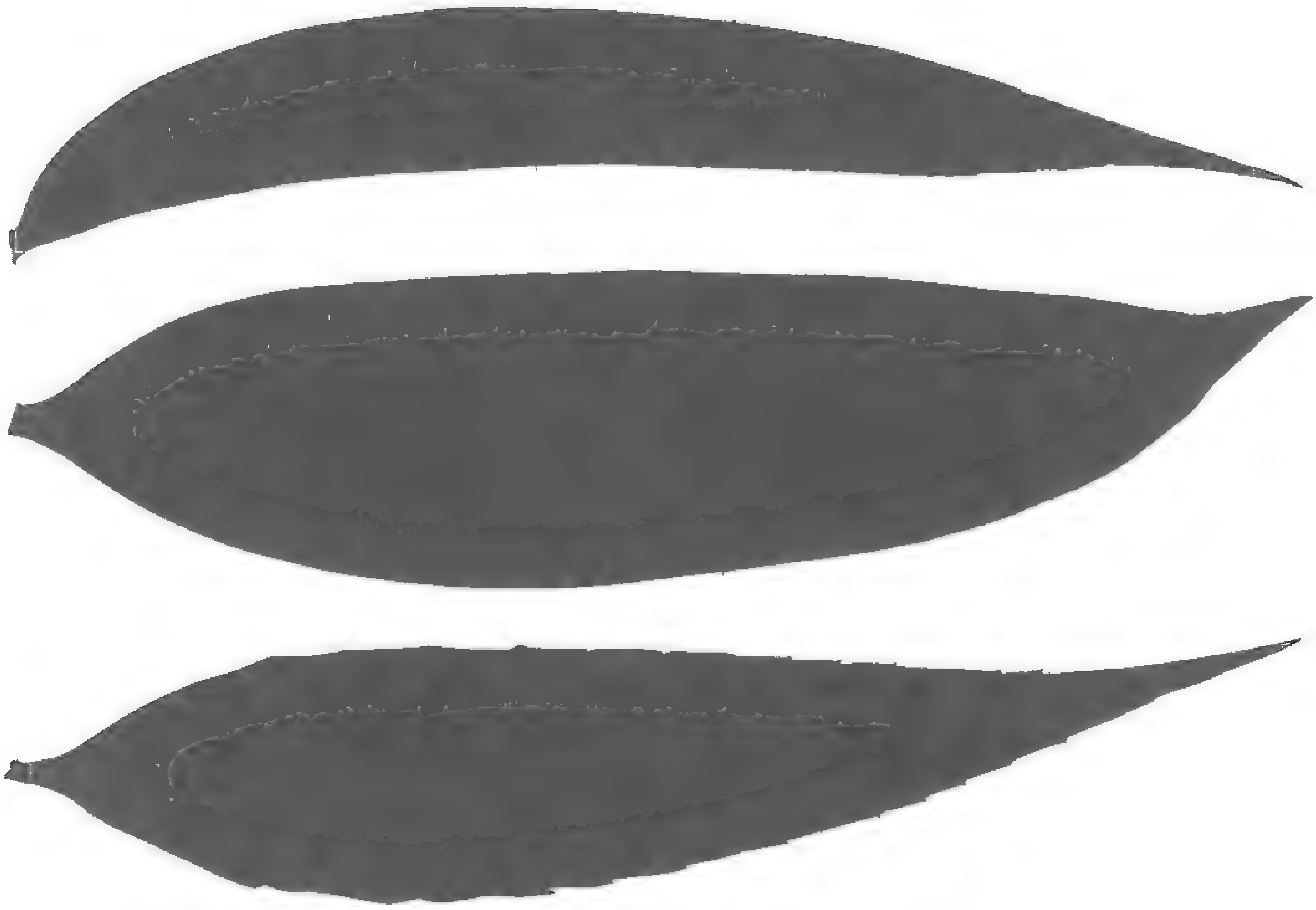

Fig. 4. Leaflet shape comparison. From top to bottom: ***Zamia decumbens, Zamia tuerckheimii, Zamia bussellii/onan-reyesii.***

understood at this time. Considering the fact that the species was described from a single cultivated individual obtained under unusual circumstances, that its present geographic distribution remains unclear, and that its megasporangiate strobili are unknown, a detailed comparison cannot currently be made between this species and *Z. decumbens*. However, based on Chamberlain's description, this species appears to have an erect stem 14 cm in diameter compared to the stems of *Z. decumbens*, which are decumbent and up to 11 cm across. In addition, *Z. monticola* is described as having 20–32 microsporangia per microsporophyll, whereas *Z. decumbens* has 12–18.

Conservation status.—Although we observed seven different populations in the Maya Mountains adding up to an extent of occurrence of 2600 km^2, the populations were all small, occupying a small area, and limited to the very specialized mountain top and sinkhole habitats. Despite visiting seven populations, only the two sinkhole populations had numerous large plants of reproductive size (about 150 each). The rest of the populations, located on rocky mountaintops, all had less than 15 individual plants of a much smaller size than those observed in the sinkholes. In total, less than 350 plants were observed within a combined area of occupancy of less than a square kilometer. Discussion with local residents throughout the range of *Z. decumbens* confirms that plants of this species have been extracted commercially in the past and seeds continue to be extracted for commercial purposes. During our fieldwork in the sinkholes, we found evidence of past mechanical removal of megasporangiate strobili, and a seemingly low number of seedling and young plants, perhaps suggesting that continued harvesting of seeds may be affecting the health of these populations. Specific locality information has been purposefully withheld from this paper in order to further minimize the risk of illegal harvesting.

Considering how fragmented the distribution of this species is, most likely resulting from its specific habitat requirements, the small number of healthy, reproductively active populations observed, the small combined area of occupancy for this species, and the evidence of past and present commercial exploitation,

TABLE 2. Summary of diagnostic characters for *Z. tuerckheimii*, *Z. bussellii/onan-reyesii*, and *Z. decumbens*.

	Z. tuerckheimii	***Z. bussellii/onan-reyesii***	***Z. decumbens***
Microstrobilus length	14–17 cm	27.5 cm	11–16.5 cm
Microstrobilus width	2.5–4 cm	3.8 cm	2.1–2.5 cm
Microstrobilar peduncle length	to 6.5 cm	8.5 cm	11–23 cm
Microsporophyll shape	Elongate triangular	Broadly triangular	Broadly triangular
Microsporangia	18–26 Arranged in two rows	40+ arranged in single row	12–18 arranged in two rows
Megastrobilus length	16.3–22 cm	22.4–25.2 cm	12–20 cm
Megastrobilus width	8.3–10 cm	10–11.2 cm	5.7–6.4 cm
Leaf length	to 2 m	to 1.51 m	to 1.75 m
Leaf number	to 20	to 40	to 17
Petiole armature	Sparse or unarmed	Light to moderate	Moderate to heavy
Leaflet length	19–30 cm	15.5–36 cm	17.5–29 cm
Leaflet number	to 14	to 23	to 28
Leaflet width	4–9 cm	3–4.4 cm	2.8–4.1 cm
Leaflet texture	Chartaceous	Papyraceous	Chartaceous
Leaflet margins	Entire or with a few minute teeth at distal end	Prominent teeth on the lower margin	Entire or with a few minute teeth at distal end
Eophyll leaflet pairs	1	4	1
Stem height	to 3 m	to 2 m	to 80 cm long.
Stem habit	Erect or leaning	Erect or leaning rotting at base and rooting horizontally	Decumbent, often

Zamia bussellii/onan-reyesii measurements derived from Schutzman et al., 2008. *Zamia tuerckheimii* measurements derived from Donnell Smith (1903), Standley & Steyermark (1958), Vannini 2008, and measurements taken by primary author. *Zamia decumbens* measurements taken *in-situ* by authors. All measurements based on mature plants.

we consider this species critically endangered and therefore recommend a Red List Category of CR for this species based on criteria B2ab (i, ii, iii, iv, v) (IUCN 2001). It should be noted that although the criteria have changed somewhat based on new information, we are recommending a continuation of the Red List category currently listed for this species under the misapplied name "*Zamia prasina.*"

ACKNOWLEDGMENTS

The Association of Zoological Horticulture (AZH) funded our research and conservation work with this species through the grant "*Zamia prasina* in Belize." Tim Gregory and Montgomery Botanical Center supported additional work in Belize.

John Janovec and Amanda Neill were the first to scientifically document and collect the sinkhole populations of *Z. decumbens*, providing the inspiration for our return to Belize on a research expedition. Green Hills Butterfly Ranch and Botanical Collections donated significant in-kind support by providing lodging, equipment and work infrastructure in Belize. The Belize Forest Department granted the scientific research and collecting permit (CD/60/3/08(45)) supporting research on Belizean Zamiaceae, as well as herbarium infrastructure for preservation of voucher specimens. Valentino Tzub and Boris Arevalo provided field assistance. Willie Tang offered to identify the possible pollinators of *Z. decumbens* and provided the images of them. Jay Vannini provided information on *Z. tuerckheimii* and comments on the manuscript. Bart Schutzman helped in the Latin diagnosis and provided comments on the manuscript. Anders Lindstromm, Chad Husby, and Alberto Sidney Taylor provided comments on the manuscript. Nancy Korber provided assistance in locating hard-to-find references. Dennis Stevenson provided herbarium specimen images and references.

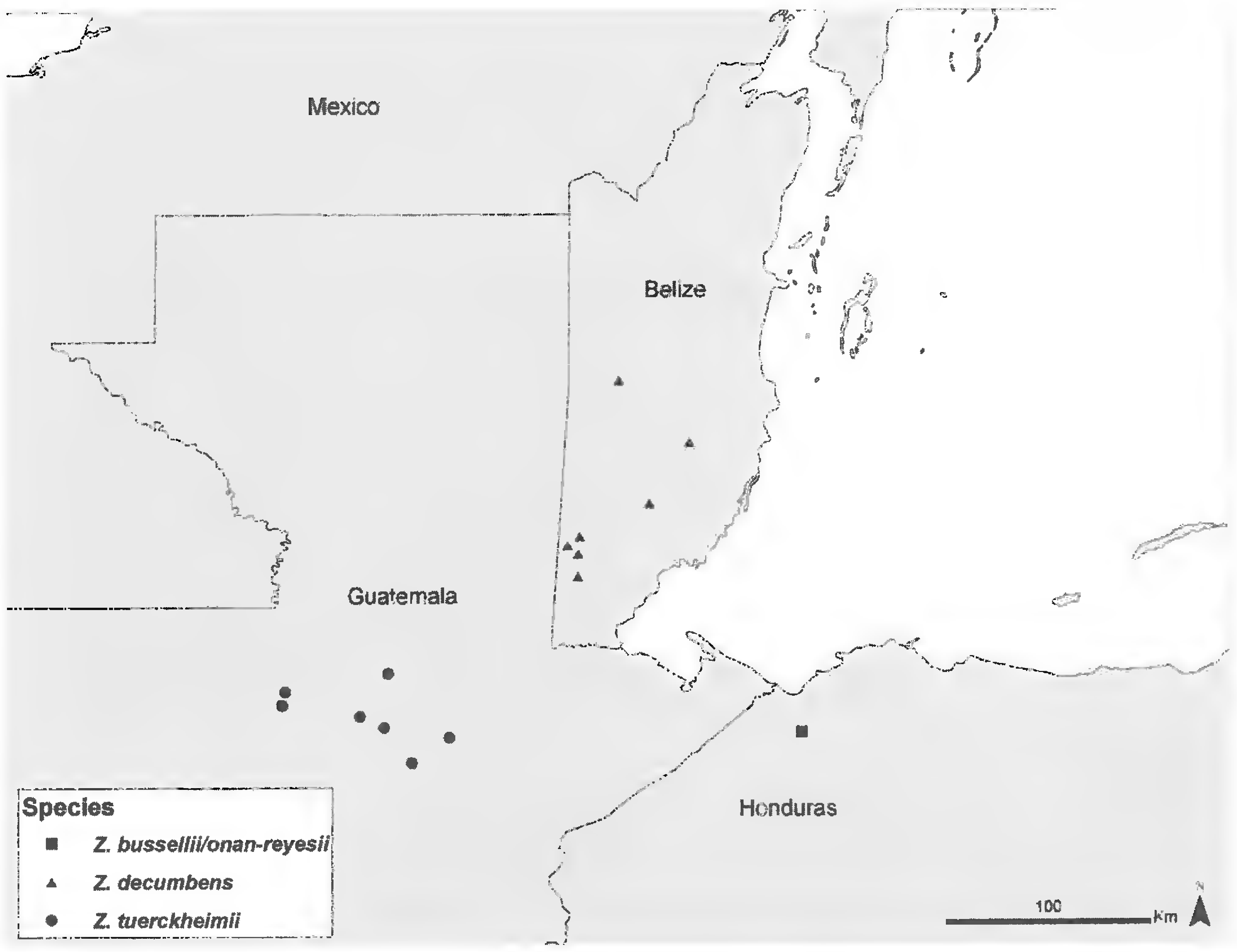

Fig. 5. Geographical distribution of *Z. bussellii/onan-reyesii*, *Z. decumbens*, and *Z. tuerckheimii*.

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BOOK REVIEW

BONNIE J. GISEL, with images by STEPHEN J. JOSEPH. 2008. **Nature's Beloved Son: Rediscovering John Muir's Botanical Legacy.** (ISBN 978-1-59714-106-2, hbk.). Heyday Books, P.O.Box 9145, Berkeley, California, 94709 U.S.A. (**Orders:** www.heydaybooks.com, 1-510-549-3564, 1-510-549-1889 fax). $45.00, 247 pp., 9 1/2" × 12 1/4".

Anyone who has read the published journals, newspaper articles, and other nature writings of John Muir is certainly impressed with his enthusiasm, and yes, his ecstasy as he explored and found plants, from mosses to ferns to conifers, all of which he considered friends as well as expressions of divinity. The author of this large book of texts and photographs follows Muir's ventures into wilderness with passages from the explorer's own works, drawings from his journals and letters, and specimens deposited in herbaria across the United States. In a way the book is a botanical biography of Muir—not definitive, as that would take volumes, but an excellent sampling of his botanical endeavors.

The author has updated the taxonomy of the illustrated plants and provided a useful, quick reference to them in the "Plant Gallery Citations," with a reduced picture, a herbarium legend, and a quotation from Muir on his discovery of each plant.

Photographer Stephen Joseph is also to be commended for his meticulous reproductions of herbarium specimens, enhancing color, adding contrast, and eliminating through editing software the labels and pasted strips that might otherwise distract.

The book is a worthy addition to all Muir collections and will be appreciated by botanists as well as lay readers of Muir's writings.—*Joann Karges, Texas Christian University Library (retired), Box 298400, Fort Worth, Texas 76129, U.S.A.*

WHAT IS *ZAMIA PRASINA* (ZAMIACEAE: CYCADALES)?

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ABSTRACT

The name *Zamia prasina* is presently being applied in the horticultural industry and systematic literature to a little known taxon from the Maya Mountains in Belize. An examination of the historical material of *Zamia prasina*, herbarium specimens, and wild *Zamia* populations in Belize leads to the conclusion that the name does not correctly apply to this taxon but instead is a valid prior name for *Zamia polymorpha* that takes nomenclatural precedence. A lectotype for *Z. prasina* is designated.

Key Words: Nomenclature, Priority, Belize, *Zamia prasina, Zamia polymorpha*

RESUMEN

El nombre *Zamia prasina* se está aplicando en horticultura y literatura sistemática a un taxón poco conocido de las Montañas Maya de Belize. Un examen del material histórico de *Zamia prasina*, en especímenes de herbario, y poblaciones silvestres de *Zamia* en Belize nos lleva a la conclusión de que no se aplica el nombre correctamente a este taxon, sino que es un nombre previo válido para *Zamia polymorpha* y por lo tanto tiene prioridad nomenclatural. Se designa un lectotipo para *Zamia prasina*.

INTRODUCTION

Zamia prasina Bull was described in 1881 in English nurseryman William Bull's horticultural catalog. Historically, this species has received little mention in the literature, but in recent years the name has been applied in the horticultural industry and systematic literature to a relatively unknown taxon from the Maya Mountains of Belize. We re-examined the historical material related to *Zamia prasina* as well as herbarium specimens and wild *Zamia* populations in Belize in order to uncover the true identity of this species, which is presented in the following analysis.

HISTORICAL MATERIAL AND EARLY USAGE OF THE NAME *ZAMIA PRASINA*

William Bull's 1881 horticultural catalog provided the following description for *Zamia prasina*:

"A handsome and distinct-looking Cycad, introduced from Honduras [referring to British Honduras, now Belize]. The stems in the young plants roundish or roundish-ovate, clothed with the imbricating scales left by the falling of the leaves. The leaves are equally pinnate, the dark green stalks terete, with an indistinct furrow in front, and furnished with a few small white prickles. The leaf-blade is oblong-ovate, pinnate, with some sixteen or seventeen pairs of oblanceolate pinnae, entire, and tapered at the base, where they are set on by a distinctly swollen articulation, denticulate towards the apex, the upper surface of a bright grass-green colour, whence the name. 1 ½ guinea."

Bull also provided a leaf of *Zamia prasina,* which was subsequently mounted as an herbarium specimen at Kew. In a letter attached to this specimen, dated March 22, 1881, he invites William Turner Thiselton-Dyer, at the time Assistant Director at Kew, to stop by his nursery and collect a leaf of *Z. prasina*. Although there was no notation on the specimen indicating when it was collected, it was probably shortly after Thiselton-Dyer received the invitation.

The specimen at Kew was annotated as a possible holotype of *Z. prasina* by Dennis Stevenson of the New York Botanical Garden on September of 1999. However, it has not been designated as a type for the species in any of the printed matter we consulted. This specimen, presumably provided by Bull the same year as he described the species in the horticultural catalog, undoubtedly represents the original material on which the species was based. However, because no reference was made to this specimen in the protologue, it cannot be considered a holotype under article 9.1 of the 2005 International Code of Botanical Nomenclature ("Vienna Code"). We remedy this situation by here designating this specimen as the lectotype for *Z. prasina*.

Zamia prasina Bull, Hort. Cat. 176:20. 1881. Type: [BRITISH] HONDURAS [BELIZE]: cultivated from Belize, *William Bull s.n.*, 22 Mar 1881 (LECTOTYPE, here designated: K!).

Zamia polymorpha D.W. Stev., A Moretti & Vázq.Torres, Delpinoa 37–38:3–8. 1998. Type: BELIZE. Cayo: 22 Jan 1989, *D. Stevenson et al. 1119* (HOLOTYPE: NY; ISOTYPES: BRH, FTG, MO, NY, U).

In addition to this specimen, there is an illustration of a leaf and caudex of *Zamia prasina* at Kew (dated 1881). A letter attached to the illustration (dated June 15, 1881) provides some background on Bull's original importation of *Zamia prasina*. The letter, addressed to "J. Smith Esq." (presumably Kew curator John Smith), mentions that a "Mr. Watson" (presumably Kew assistant curator William Watson) "talked him out of two plants that he did not want to give up." He also mentions receipt of two separate shipments of *Zamia* from Belize and that each of the plants taken by Mr. Watson came from a separate shipment. The first plant, described as having "widely separate" leaflets was the only surviving plant from one of the shipments. The second plant, which Bull called *Z. prasina*, was one of the larger plants from the second shipment of which only a few plants survived. Mr. Bull clearly did not want to let go of the two plants and was asking Mr. Smith to return them. In return, he promised to provide "a couple" of the smaller surviving plants of *Z. prasina* for the collection at Kew. The illustration appears to be traced from the original *Z. prasina* plant provided by Bull before it was returned, as it is on a herbarium-specimen-sized sheet and bears the hand-written words "returned *Zamia prasina*." Another inscription on the illustration reads "cf. *Z. latifolia* Lodd.," and an inscription on the herbarium specimen reads "*Z. latifolia* Lodd." These notes, in the same handwriting, were most likely added by Thiselton-Dyer, as he included *Z. prasina* in his treatment of Mexican and Central American cycads (Thiselton-Dyer 1884) as a synonym of *Z. latifolia* Lodd. ex A.DC (see de Candolle 1868). Thiselton-Dyer added a question mark next to his listing of *Zamia prasina* indicating he was uncertain about its synonymy with *Z. latifolia*. In fact, today it is not entirely clear what *Z. latifolia* is, as it was a horticultural name from Loddiges' catalog for which no type specimen or illustration was provided. Miquel (1843) considered *Zamia latifolia* a synonym of *Z. muricata* var. *obtusifolia*, later bringing it to species rank (1849). In 1847, when he still considered *Z. latifolia* a variety of *Z. muricata*, he published an illustration of a leaflet labeled *Zamia latifoliae* (Linnaea 19(4): Tab. VII, fig. a. 1847), which Stevenson and Sabato (1986) selected as the neotype for *Z. muricata* var. *obtusifolia* (Fig. 1a). Since so little is known about the true identity of what was originally called *Z. latifolia* in Loddiges's catalog, it must be considered a *nomen dubium* as well as its synonym, *Z. muricata var. obtusifolia*. Furthermore, the leaflet illustrated in Miquel's publication is unlikely to have been derived from a Belizean species, as none of the known species have leaflets with strongly serrated rounded leaflet tips. The leaflet shape and serrations in Miquel's illustration match closely those of *Z. furfuracea* plants at Montgomery Botanical Center grown from seed collected near Alvarado, Veracruz, Mexico (Fig. 1b).

Thiselton-Dyer clearly considered Bull's specimen to be different than *Z. muricata* Willd., as both species are compared on the *Zamia prasina* illustration in the same handwriting as the "*Z. latifolia*" annotations. The comparison indicates that *Z. prasina* has leaflets that are coriaceous, abruptly acuminate, and serrulate at the apex, whereas *Z. muricata* has leaflets that are chartaceous, gradually acuminate, and spinulose-serrate towards apex. *Zamia muricata* was originally described from Venezuela, and as currently circumscribed, is a species occurring only in Venezuela and Colombia.

In his 1932 cycad treatment, Schuster listed *Z. muricata* var. *obtusifolia* as well as *Zamia prasina* as synonyms of *Z. loddigesii* var. *latifolia* (Lodd.) J. Schust., incorrectly citing the publication date for Bull's horticultural catalog as 1822 rather than 1881 (Schuster 1932).

MODERN USAGE OF THE NAME *ZAMIA PRASINA*

Since Schuster's synonymization of *Zamia prasina*, the species name received little use until recent years, as apparently the original description and Bull's specimen were misplaced and not re-discovered until 1998 (Whitelock 2002). Since then, the name has been misapplied to a rare and little known taxon from isolated localities in the Maya Mountains of Belize (see Balick et al. 2000; Whitelock 2002; Janovec & Neill 2003; Hill 2004). This species, formally described in this issue (Calonje et al., page 31), differs from *Zamia prasina* in having an epigeous stem, leaflets that are chartaceous, gradually acuminate, with a raised longitudinal

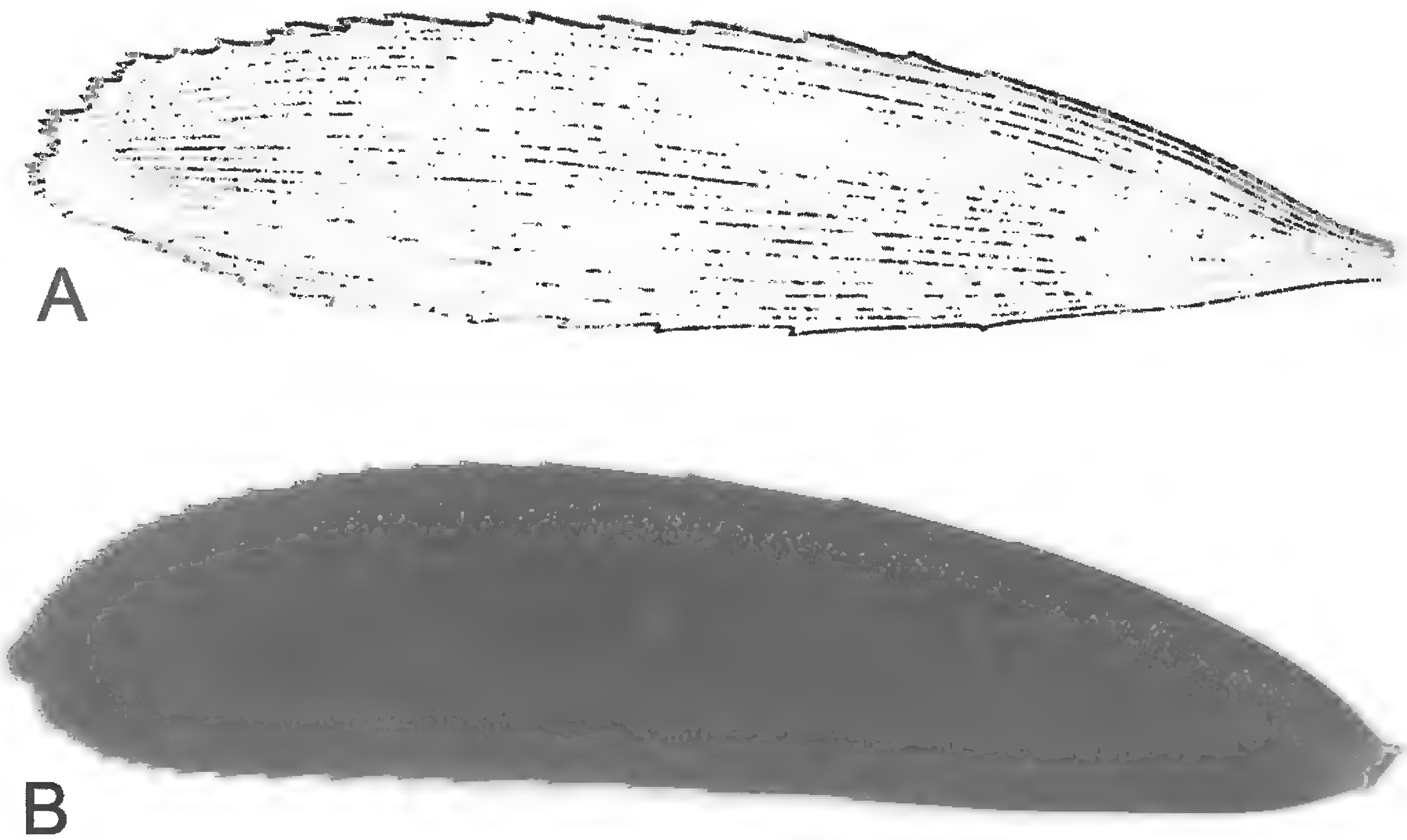

Fig. 1. A. Leaflet of *Zamia muricata* var. *obtusifolia* (= *Zamia latifolia*) illustrated in Miquel (1847), B. Leaflet of *Zamia furfuracea* from plant collected near Alvarado, Veracruz, Mexico (MBC Accession # 20011305*A).

crease, and margins that are entire or with few minute teeth at the apex, rather than a hypogeous stem and leaflets that are coriaceous, abruptly acuminate, without a raised longitudinal crease, and strongly serrulate on the upper half (Fig. 2).

Since it is clear that the plant currently being called *Z. prasina* in horticulture and recent literature does not match the original description, lectotype or illustration of this species at Kew, then the logical ensuing question to ask is: What is *Zamia prasina*?

The only other described *Zamia* species currently known from Belize are *Z. variegata* Warsz. and *Z. polymorpha* D.W. Stev., A. Moretti & Vázq.Torres. While *Zamia variegata* has strongly serrulate leaflets as described in the protologue for *Z. prasina*, these are papyraceous rather than coriaceous, and are variegated with yellow flecks, a unique and horticulturally appealing character that Bull undoubtedly would have mentioned in his horticultural catalog. However, the coriaceous, strongly serrulate leaflets of *Zamia polymorpha* exactly match the description of *Zamia prasina*.

SYNONYMIZATION OF *ZAMIA POLYMORPHA*

Zamia polymorpha as currently circumscribed ranges from the Yucatan Peninsula in Mexico to Belize (Stevenson et al. 1998). It was previously considered to be a form of *Z. loddigesii* Miq. with a highly variable karyotype (see Vovides & Olivares 1996). Stevenson et al. (1998) noted the karyotype variability as an important characteristic of this species in addition to its high level of polymorphism in leaf and leaflet morphology. This variability was ascribed to phenotypic plasticity due to differences in sun exposure, with plants exposed to full sun having shorter and narrower leaves with lanceolate leaflets, those growing in deeper shade having longer, broader leaves with elliptic to suboblanceolate leaflets, and those growing in intermediate conditions displaying leaf morphologies that are intermediate between the two extremes.

During a cycad research expedition to Belize in August of 2008 sponsored by Montgomery Botanical Center, an extensive survey of populations matching Stevenson et al.'s description of *Z. polymorpha* with strongly serrulate leaflets uncovered some populations with remarkably consistent vegetative morphology, and others that were highly variable. The morphologically consistent populations included narrow-leafleted

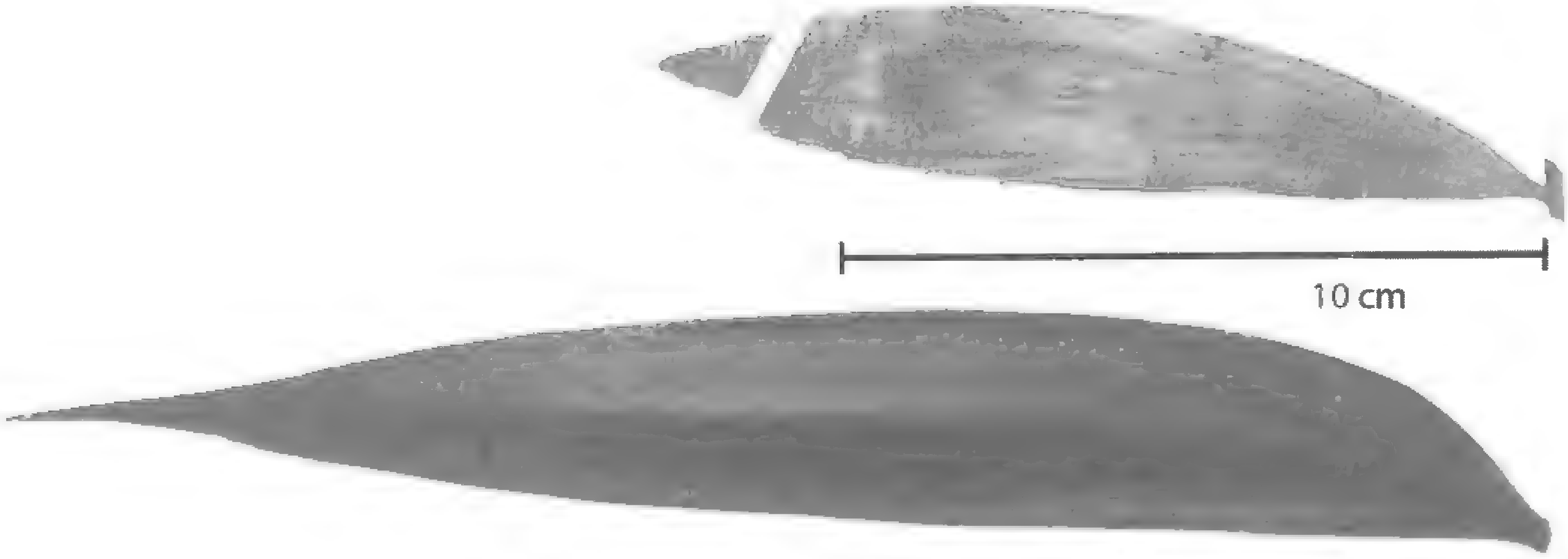

Fig. 2. Same-scale comparison of leaflet of *Zamia prasina* from holotype (above) and leaflet from *Zamia* sp. erroneously referred to as *Z. prasina* (below, *Michael Calonje et al. BZ08-201*).

plants growing in savannas closely resembling *Zamia loddigesii*, and also other populations growing in tropical evergreen seasonal broad-leaved forests with larger leaves and wider leaflets. In addition to these morphologically consistent populations, others were found to be highly variable, containing the two forms mentioned above as well as intermediate plants.

The variability in these mixed populations appeared to be at least partially genetically determined, as plants with wide leaflets were sometimes found growing in full sun, and some narrow-leaflet plants were found growing in more shaded areas. Plants with narrow leaflets collected in an open savanna by the second author have retained their morphological characteristics despite years of growing in a shaded environment at Green Hills Botanical Collections.

A survey of one highly variable population halfway between Belmopan and Belize City uncovered individual plants closely matching Bull's holotype (Fig. 3) of *Zamia prasina* and the drawing of this species at Kew (Fig. 4), as well as the holotype for *Z. polymorpha* (Fig. 5), indicating that *Z. prasina* and *Z. polymorpha* are the same species, and therefore *Z. prasina* takes nomenclatural precedence over *Z. polymorpha*.

In addition, there is also some circumstantial evidence suggesting that *Z. prasina* is a prior valid name for the species now considered *Z. polymorpha*. William Bull did not provide a locality or specific habitat information for where in Belize *Z. prasina* may have been collected, but two years after its description, Morris (1883) identified plants common on ridges and banks near Point Ycacos as belonging to this species. Morris did not provide a description or illustration of the plants he saw, but the cycad that is common in this area, visited by the second author, matches the description of *Zamia polymorpha*. Furthermore, this species is the most common cycad throughout Belize and would very likely be the first species encountered by collectors for William Bull.

Zamia prasina (now including *Z. polymorpha*) appears to belong to a species complex that includes *Z. loddigesii* and other related species such as *Z. paucijuga* Wieland, and *Z. spartea* A. DC (Schutzman 1987). Members of this species complex display high levels of morphological variation (Gonzalez-Astorga et al. 2006) and may easily hybridize (Schutzman 1987). Although Schuster's (1932) taxonomic work with cycads is not highly regarded (see Stevenson & Sabato 1986; De Luca 1990; Taylor et al. 2008), his inclusion of *Z. prasina* as a synonym of *Z. loddigesii* suggests that the name at the time may have been applied to plants within this species complex.

The differential morphological variability observed within populations of *Zamia prasina*, coupled with the high morphological variability between populations and the variable karyotypes reported by Stevenson and Sabato (1986), indicate that while it is possible that populations with subterranean stems and coriaceous, serrulate leaflets represent one highly polymorphic species, further research including genetic sampling

Fig. 3. Same-scale comparison of *Zamia prasina* lectotype (right) and specimen collected between Belmopan and Belize City (left, *Michael Calonje et al. BZ08-086*).

across a wide range of populations will be needed to better clarify the relationship between the different forms and their placement within the *Zamia loddigesii* species complex. Until species limits are clarified we recommend continued recognition of *Zamia prasina* (with *Z. polymorpha* included within its circumscription).

ACKNOWLEDGMENTS

Funding in support of the 2008 Belize expedition was generously provided by the Association of Zoological Horticulture (AZH), Tim Gregory, and Montgomery Botanical Center (MBC). Green Hills Botanical Collections donated significant in-kind support by providing lodging, equipment and work infrastructure in Belize. Patrick Griffith, Chad Husby, Anders Lindstrom, Walter S. Judd, and Bart Schutzman provided comments on draft versions of the manuscript. The Belize Forest Department granted the scientific research and collecting permit (CD/60/3/08(45)) supporting research on Belizean Zamiaceae, as well as herbarium infrastructure for preservation of voucher specimens. Dennis Stevenson and Andrew Vovides provided images of historical material of *Zamia prasina*. Nancy Korber of Fairchild Tropical Botanical Garden graciously assisted me in the search of references.

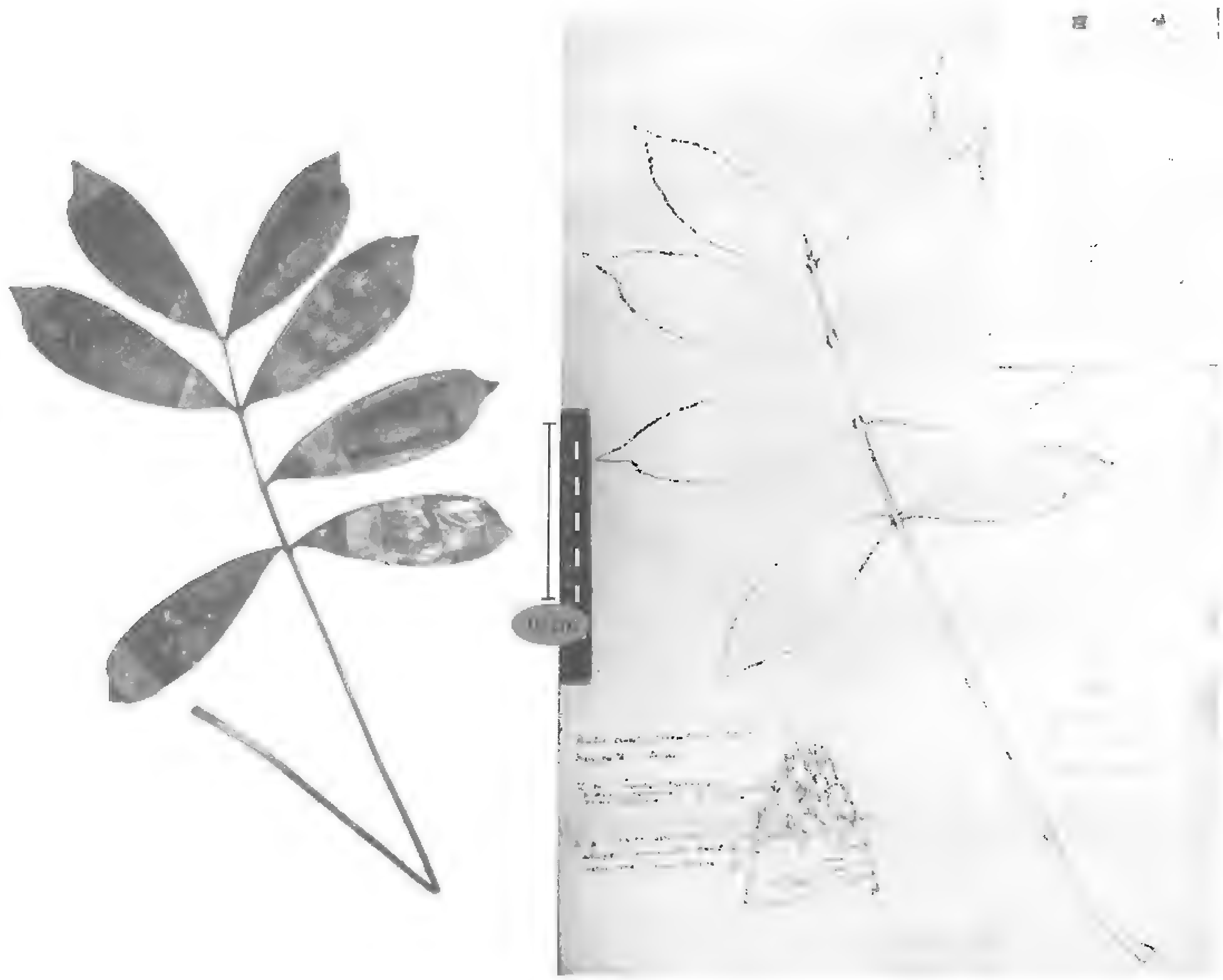

Fig. 4. Same-scale comparison of *Zamia prasina* drawing at Kew made from plant supplied by William Bull (right) and specimen collected between Belmopan and Belize City (left, *Michael Calonje et. al BZ08-073*)

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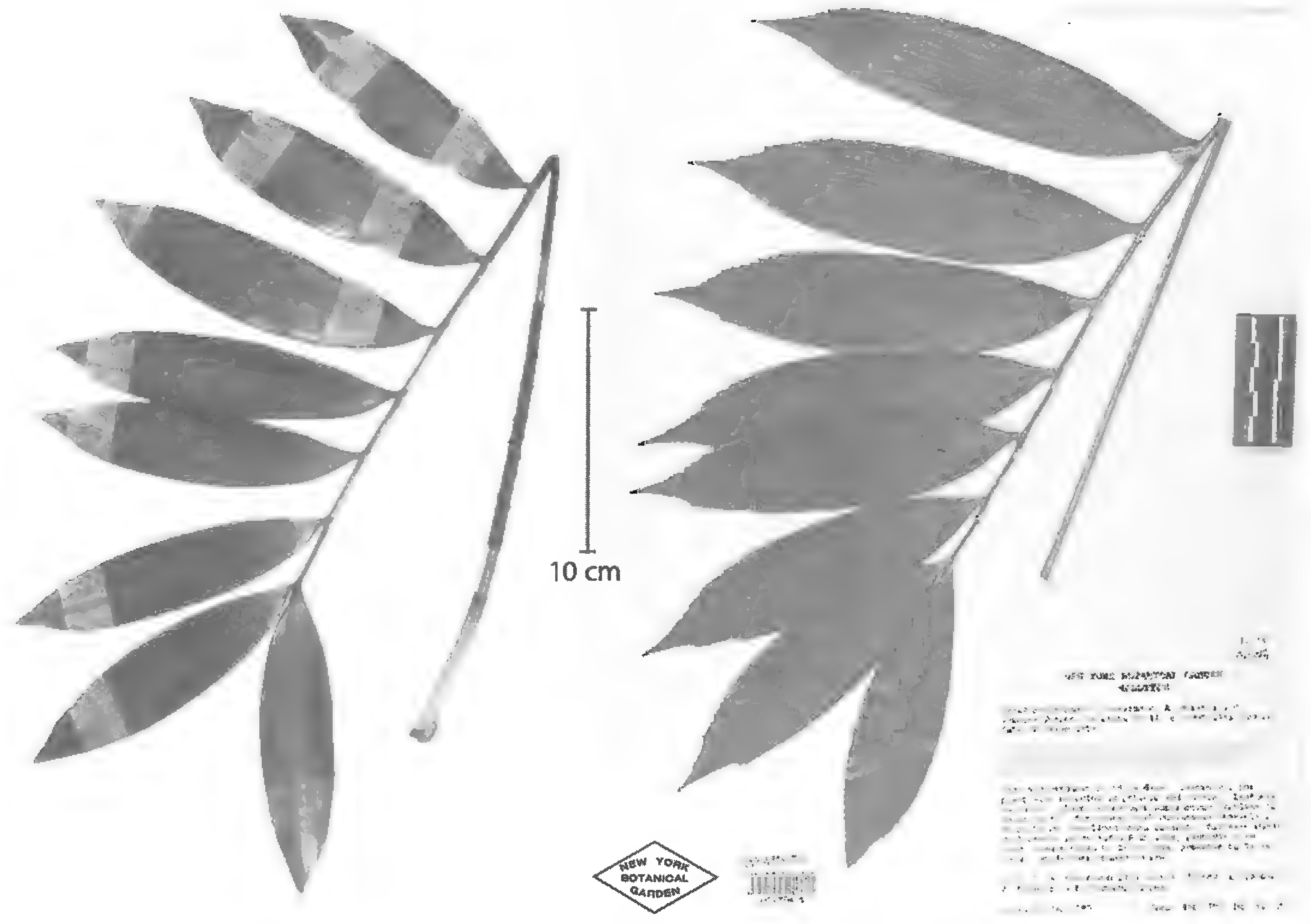

Fig. 5. Same-scale comparison of *Zamia polymorpha* holotype (right) and specimen collected near between Belmopan and Belize City (left, *Michael Calonje et. al BZ08-085*). Image of *Zamia polymorpha* holotype used with permission from The C.V. Starr Virtual Herbarium of the New York Botanical Garden (http://sciweb.nybg.org/science2/VirtualHerbarium.asp). Locality data intentionally obscured.

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BOOK REVIEWS

Roy C. Dicks (ed.). 2008. **Rhapsody in Green: the Garden Wit and Wisdom of Beverley Nichols.** (ISBN 978-03812-9485, hbk.). Timber Press, 133 S.W. Second Ave., Suite 450, Portland, Oregon 97204-3527, U.S.A. (**Orders:** www.timberpress.com, 1-800-827-5622, 1-503-227-3070 fax). $17.95, 135 pp., 6" × 7 1/2".

This little book is for aficionados of garden writer Beverley Nichols, most of whose works have recently been reprinted and from which the editor has chosen selections. Readers will take pleasure in his metaphors (fuchsias "with their white petticoats and crimson ruffs") and his likes and dislikes among the plants (disdain for *Datura*, which reminds him "of a clump of laurels on which somebody has hung the weekly washing."). For the most part the selections are cute aphorisms, sage advice, and amusing observations. —*Joann Karges, Texas Christian University Library (retired), Box 298400, Fort Worth, Texas 76129, U.S.A.*

Barbara L. Wilson, Richard Brainerd, Danna Lytjen, Bruce Newhouse, and Nick Otting of the *Carex* Working Group. 2008. **Field Guide to the Sedges of the Pacific Northwest.** (ISBN 9780870711978, pbk.). Oregon State University Press, 121 The Valley Library, Corvallis, Oregon 97331, U.S.A. (**Orders:** http://oregonstate.edu/dept/press/, 1-800-426-3797). $35.00, 431 pp., 6" × 9".

The *Field Guide to the Sedges of the Pacific Northwest* is the first illustrated guide for all 164 species, subspecies, and varieties in the genus *Carex* that occur in Oregon and Washington and throughout the Pacific Northwest. Sedges can be challenging to identify with differences between species based on small, technical characters. These differences are addressed for each species to facilitate identification.

The *Field Guide* is divided into three main parts: (1) information about sedge ecology, habitat management and restoration, ethnobotanical uses, and propagation; (2) identification key; and (3) species accounts. The primary portion of the book is the species accounts, with each species receiving a description, a distribution map, and three or more illustrations, mostly color photographs with a few botanical line drawings. In addition, there are collecting tips, a glossary, and bibliographical references.

The *Field Guide* provides a comprehensive and essential resource for botanists, land managers, restoration ecologists, and plant enthusiasts. And, as the genus *Carex* becomes increasingly important amongst landscapers, nurseries, and gardeners, the guide will serve as a handy tool for choosing Northwest natives for the garden. A very useful book with a binding that allows for easy opening. Recommended for public libraries, schools, and research organizations.

About the Authors: The *Carex* Working Group (Barbara L. Wilson, Richard Brainerd, Danna Lytjen, Bruce Newhouse, and Nick Otting) is made up of Oregon botanists fascinated by sedges and other difficult-to-identify plant groups. The CWG came together in 1993 to map the distribution of Oregon's sedges and incorporated in 2002. That effort cumulated in the publication of *Atlas of Oregon Carex* (1999). In addition to writing about and photographing sedges, the CWG contracts with public agencies and private companies to do plant inventories, plant identification workshops, and taxonomic research on plants of the western U.S.—*Gary L. Jennings, Librarian, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

FESTUCA ALOHA AND *F. MOLOKAIENSIS* (POACEAE: LOLIINAE), TWO NEW SPECIES FROM HAWAI'I

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ABSTRACT

Festuca aloha, sp. nov. of Kaua'i and **F. molokaiensis,** sp. nov. from Moloka'i are described and illustrated. The two species are endemic to the Hawaiian archipelago and grow on steep mountain slopes and volcanic cliffs with other native mesic flora. A key to the species of *Festuca* found in the Hawaiian Islands is given.

Key Words: *Festuca*, new species, Hawaii, Loliinae, key

RESUMEN

Se describen e ilustran **Festuca aloha,** sp. nov. de Kaua'i y **F. molokaiensis,** sp. nov. de Moloka'i. Las dos especies son endémicas del archipiélago de Hawaii y crecen en acantilados volcánicos y en laderas montañosas pendientes junto con otra flora autóctona de ambientes mésicos. Se proporciona una clave de identificación de las especies de *Festuca* que habitan en las islas del archipiélago.

While revising specimens of *Festuca* deposited at the United States National Herbarium (US) the first author found two specimens of fine-leaved individuals from Kaua'i that were identified as *F. rubra* L. However, these individuals exhibit several characters that separate them from holarctic red fescues of the *F. rubra* complex, including: leaf blades flat with involute margins, sheaths open, relatively long ligules, and ovaries with densely hairy apices. After reviewing specimens of *Festuca* from Molokai'i deposited at the Bishop Museum (BISH) we noticed an additional taxon. Previously, the only species of *Festuca* and relatives recorded from Hawai'i and the Pacific include the endemic, *F. hawaiiensis* Hitchc. (Hitchcock 1922), a robust broad-leaved species placed in *F.* subg. *Drymanthele* V.I. Krecz. & Bobrov sect. *Banksia* E.B. Alexeev (Alexeev 1980), and three Eurasian species: the fine-leaved *F. rubra* L. (*F.* subg. *Festuca* sect. *Aulaxyper* Dumort.); and the broad-leaved *F. arundinacea* Schreb. and *F. pratensis* Huds. [*F.* subg. *Schedonorus* (P. Beauv.) Peterm. sect. *Schedonorus* (P. Beauv.) Endl]. The taxonomy of *Festuca* s.l., the largest genus of monophyletic subtribe Loliinae Dumort., is in a state of flux. Much additional research is needed to properly align the taxa, although preliminary data from DNA sequencing (Catalán et al. 2007; Inda et al. 2008) suggest that two major clades may exist. As elements of the "broad-leaved" clade, the latter two species have been classified within the separate genus *Schedonorus* P. Beauv., as *Schedonorus arundinaceus* (Schreb.) Dumort and *S. pratensis* (Huds.) P. Beauv. (Soreng et al. 2003; Snow 2008). In addition, *Festuca* subg. *Drymanthele* is sometimes recognized as the genus *Drymochloa* Holub. The "fine-leaved" clade of fescues, including *F. rubra*, are placed in *Festuca* s.s. (Soreng et al. 2003). However, results are still equivocal concerning the resolution of the division at the base of the two major clades.

Specimens were examined from the Bishop Museum (BISH), National Tropical Botanic Garden (PTBG), Missouri Botanical Garden (MO), and the United States National Herbarium (US).

Festuca aloha Catalán, Soreng & P.M. Peterson, sp. nov. (**Figs. 1A–J, 2**). Type: U.S.A. Hawaii: Kaua'i, Hanalei district, Kalalau Rim, Kalalau side below and W of the first Kalalau lookout, isolated hanging side-valley of lowland diverse mesic forest surrounded by precipitous cliffs, associated with species of *Gouania, Peucedanum, Poa mannii, Hedyotis, Lysimachia glutinosa, Melicope pallida, Nototrichium, Dubautia, Dryopteris, Metrosideros, Lipochaeta subcordata, Lobelia niihauensis, Lipidium, Nestegis, Hibiscus kokio, Eragrostis, Santalum, Myrsine, Acacia,* and *Psychotris,* 790 m, 13 Mar 1992, *K.R. Wood 1701 & S. Perlman* (holotype: PTBG-17679; isotype: US-3252239).

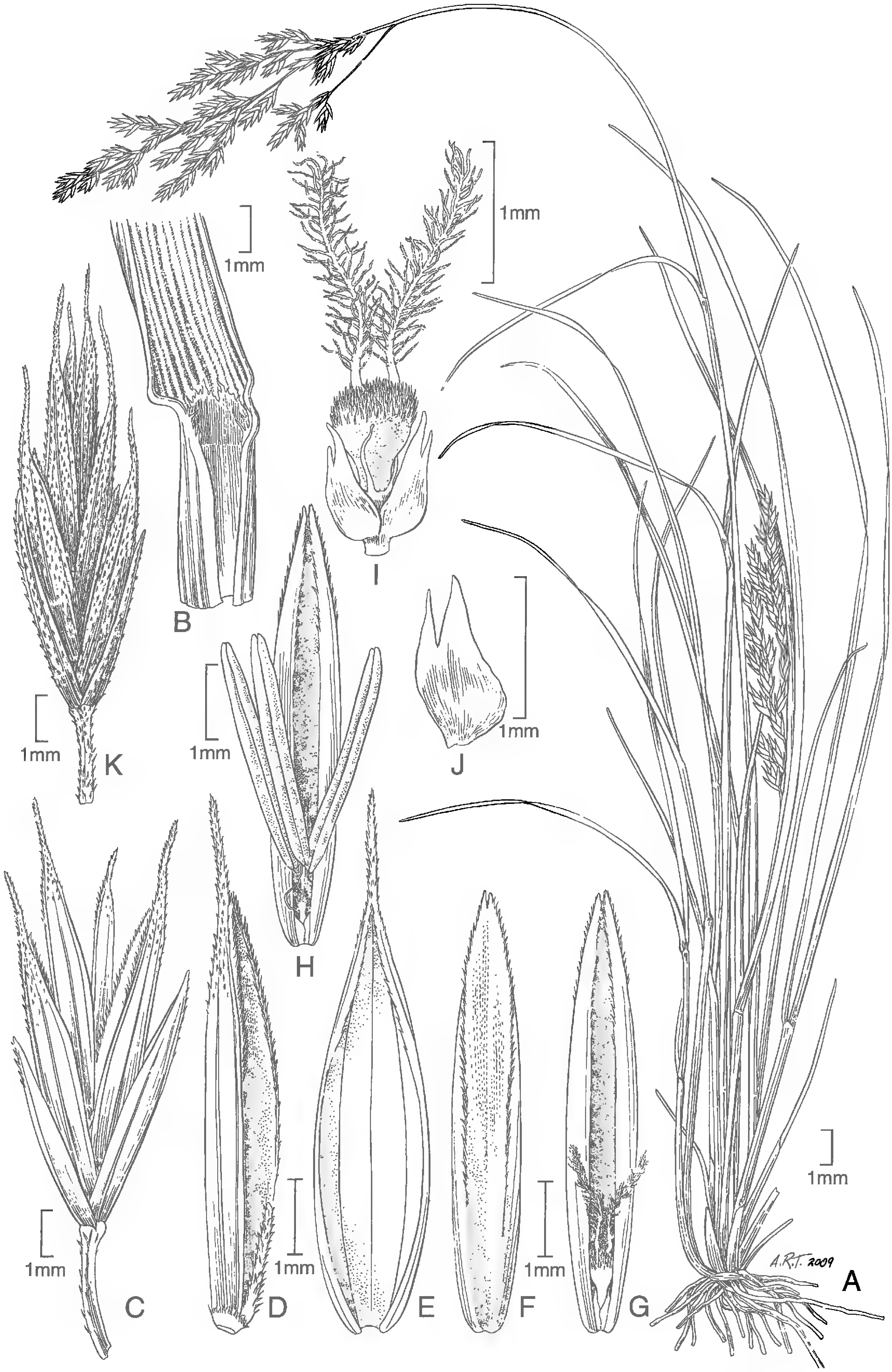

Fig. 1. Illustration of *Festuca aloha* Catalán, Soreng & P.M. Peterson (isotype, US-3252239). A. Habit. B. Sheath, ligule, and blade. C. Spikelet. D. Floret with rachilla. E. Lemma, ventral view. F. Palea, dorsal view. G. Palea with ovary, ventral view. H. Palea with immature ovary and mature stamens, ventral view. I. Lodicules, mature ovary, and basal remnant of filaments. J. Lodicule. *Festuca molokaiensis* Soreng, P.M. Peterson & Catalán (holotype, BISH-728771). K. Spikelet.

A *Festuca hawaiiensis* Hitchc. paniculis 8–11 cm longis, angustibus, ramis erectis, ascendentibus; pedicellis (1–)1.5–3.5(–5) mm longis; lemmatibus 5.8–8 mm longis; laminis 1.5–2.4 mm longis, recedit.

Plants perennial, cespitose, with extravaginal innovations; cataphylls conspicuous, brownish. **Culms** 45–70 cm tall, erect, slender (ca. 1 mm diam.), nodes 2–3, smooth and glabrous. **Leaf sheath** margins fused for 1–2 mm at base, overlapping more than ½ the length below, sparsely villose abaxially when young, becoming glabrous at maturity, purple-brownish at the base, greenish above, becoming fibrous in age at base; **auricles** absent; collars glabrous; **ligules** 1–1.5 mm long, scarious, glabrous, brownish, apex obtuse, dentate-erose; **leaf blades of vegetative shoots** 22–33 cm × (1–)1.5–1.7 mm, erect to pendant, flat with involute margins, glabrous and smooth abaxially, hirsute along protruding ribs adaxially, the hairs up to 0.1 mm long, cross section (Fig. 2) about 1 mm bearing 13–16(–20) larger vascular traces or veins, each with prominent ribs adaxially alternating with smaller ribs on the secondary and tertiary veins, **sclerenchyma** strands forming trabeculae or girders on most veins; **leaf blades of culms** about 22 cm × 2.4 mm, erect to pendant. **Panicles** 8–11 × 2.5–4 cm, erect, axis and peduncle smooth; loosely contracted with 34–66 spikelets, spikelets mostly at branch tips; panicle branches 2(3) per node, basal branches 4–6 cm and ca. 1/2 the length of panicle, angled, erect or ascending, smooth proximally to scabrous, angled distally. **Spikelets** 8.2–13 mm × 3.5–6.0 mm, 4–6-flowered, broadly lanceolate, pale green, sometimes tinged with purple; pedicels (1–)1.5–3.5(–5) mm long; rachilla internodes 0.8–1.2 mm long, scabrous; **glumes** lanceolate, green, margins very narrowly scarious (<0.5 mm), apex acute; **lower glumes** (3.6–)3.9–4.2(–4.5) mm long, 1-veined; **upper glumes** 5.2–5.5(–6.0) mm long, 3-veined; **lemmas** 5.8–8.0 mm long, 5-veined, glabrous below, scabrous near the apex, green or tinged with purple at the apex, mucronate to awned, the mucro or awn 0.5–1.1 mm long, scabrous; callus rounded, obliquely angled (to 45°), smooth to dorsally minutely scabrous at the apex; **paleas** longer or shorter than lemma, scabrous on and between keels; stamens 3, **anthers** 3.1–4.2 mm long; **ovary** densely hairy on upper 1/3. **Caryopsis** not seen.

Additional material examined. **U.S.A. Hawai'i. Kaua'i:** Hanalei district, Kalalau Rim, N of Kahuamaa flat, 990–1020 m, 3 Mar 1991, *K.R. Wood 631, M. Query, S. Montgomery* (PTBG-9498); north aspect, 1060–1190 m, 5 Apr 1991, *K.R. Wood 901 & M. Query* (PTBG-13876); Kalalau side below and W of the first Kalalau lookout, 13 Mar 1992, *K.R. Wood 1704 & S. Perlman* (PTBG-17678, topotype); Honopu Rim, undisturbed cliffs, rare, with old inflorescence, growing in clumps, seen with *Panicum lineale*, 2800 ft, 6 Nov 1993, *K.R. Wood 2832* (PTBG-29690; MO-4639044); Kalalau valley, Clumping on N facing basalt cliffs, seen with *Poa mannii, Panicum lineale, Eragrostis variabilis, Carex meyenii*, ca. 3000 ft, 17 Jun 1994, *K.R. Wood 3245* (PTBG-20438); Pohakuao, hanging valley between Kalalau and Hanakoa, below Puu Ki and Kaaalahine Ridge, 2000 ft, 4 Jan 1992, *K.R. Wood 1761, S. Perlman & J. Lau* (BISH-621133, PTBG-12875, US-3250261); Waimea district, with *Panicum lineale* and *P. beecheyi*, 2000 ft, 30 Mar 1993, *K.R. Wood 2470, & S. Perlman* (PTBG-18788), *K.R. Wood 2471 & S. Perlman* (PTBG-18779); Awaawapuhi valley, N facing slopes above stream, 0.5 mi along trail, growing with *Wilkesia gymoxiphium* and *Lipidium serra*, 3300–3500 ft, 18 May 1994, *K.R. Wood 3193, S. Perlman & M. Hartley* (PTBG-15270); Upper Kawaiiki: Kaluahaulu Ridge (Mohihi-Waialae trail), W of trail along with swept rim, drop into drainage, *Acacia koa–Metrosideros polymorpha* mixed mesic forest with *Dubautia laevigata, Dianella sandwicensis, Poa sandwicensis, Schiedea stellarioides, Peperonia macraeana,* and *Claoxylon sandwicense*, 1149 m, 14 Nov 1996, *K.R. Wood 7605* (PTBG-42661).

Comments.—*Festuca aloha* has panicles 8–11 cm long, narrow, branches erect and ascending; lemmas 5.8–8 mm long; and leaf blades 1.5–2.4 mm wide; in contrast *F. hawaiiensis* has panicles 30–40 cm long, widely open, branches patent or patent-erect; lemmas 9 mm long; and leaf blades 2–3 mm wide.

The illustrator Alice Tangerini noticed that all florets with mature anthers of *F. aloha* contained small, undeveloped ovaries (Fig. 1H). Mature ovaries with well-developed styles were found only in florets that had already shed their anthers (filaments were still present) [Fig. 1I]. Therefore, *F. aloha* is apparently protandrous.

Etymology.—The specific epithet *F. aloha* name derives from the Kalalau mountains of Kaua'i.

Conservation status.—*Festuca aloha* has been found in at least six different localities of Kauaii, covering a distribution area of approximately 700 km^2. The number of individuals varies among populations but usually there are less than 1000 individuals per population. Based on these preliminary data, the new species clearly falls within Vulnerable (VU) category as defined by the IUCN (2001). The major threats to individuals of *F. aloha* are the allochthonous plants, such as: *Cyperus meyenianus* Kunth, *Erigeron* sp., *Kalanchoe pinnata* (Lam.) Pers., *Lantana camara* L., *Melia* sp., *Passiflora mollissima* (Kunth) L.H. Bailey, *Rubus*

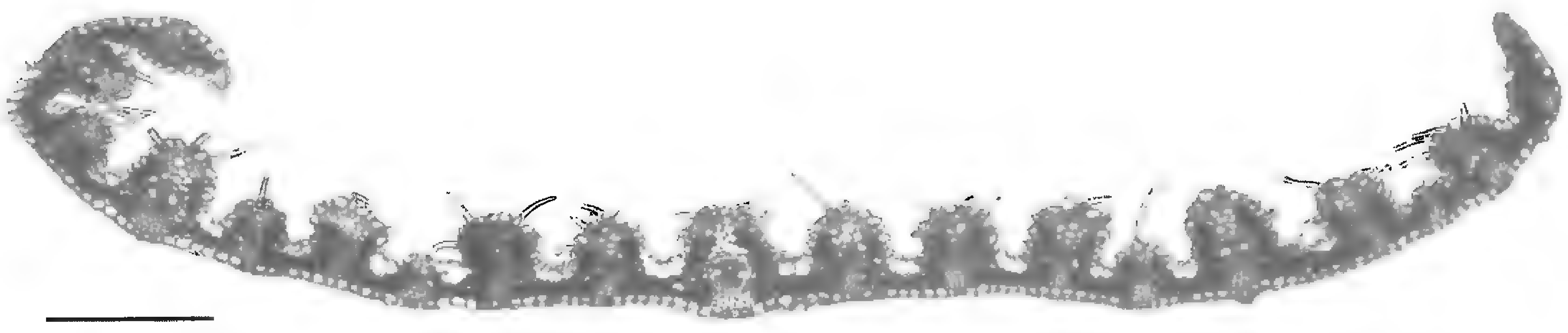

Fig. 2. Leaf blade cross section of vegetative shoots of *Festuca aloha* Catalán, Soreng & P.M. Peterson (US-3252239). Scale bar = 0.1 mm.

rosifolius Sm. ex Baker, *Setaria gracilis* Kunth, *Triumfetta* sp.; and goats and pigs (K.R. Wood, on herbarium label).

Festuca molokaiensis Soreng, P.M. Peterson & Catalán, sp. nov. (**Fig. 1K**). Type: U.S.A. Hawai'i. Moloka'i: Kupaia Gulch, on steep slopes in mesic forest, occasional, associated vegetation: *Metrosideros, Coprosma, Leptecophylla, Dodonaea, Alyxia, Viola, Melicope, Myrsine, Diospyros, Dryopteris, Phyllanthus, Luzula, Selaginella,* and *Carex*, 21.119564 N 156.936999 W, 880 m, 3 Apr 2007, *H.L. Oppenheimer H40704, S. Perlman & N. Tangalin* (holotype: BISH-728771).

A *Festuca aloha* Catalán, Soreng & P.M. Peterson, paniculis et spiculis magis gracilis et scabris, lemmatibus omnino scabris, arista longiori 1.5–2.8 mm, antheris brevioribus 2–3 mm, glumis inferis (5.0–)5.2–5.5(–5.7) mm, glumis superis (6.0–)6.2–6.8(–7.0) mm, differt.

Plants perennial, cespitose, with extravaginal innovations; cataphylls conspicuous, brownish. **Culms** up to 60–70 cm tall, scabrous below panicle. **Leaf sheaths** with margins fused for 1–2 mm at base, overlapping more than ½ the length below, purple-brownish at the base, greenish above, becoming fibrous at base in age; **auricles** absent; collars glabrous; **ligules** 1.5–2.5 mm long, scarious, glabrous, brownish, apex obtuse, dentate-erose; **leaf blades of vegetative shoots** approximately 34 cm × 2 mm, more or less pendant, flat with involute margins, glabrous and smooth abaxially, hirsute along protruding ribs adaxially and on margins and apex, dull green, cross section similar to that of *F. aloha*, about 2 mm wide bearing 25 larger vascular traces or veins, each with prominent ribs adaxially alternating with smaller ribs on the secondary and tertiary veins, bulliform cells between adaxial ribs, **sclerenchyma** strands present forming trabeculae or girders on most veins, sclerenchyma strands with thin cell walls (adaxially) and thick cell walls (abaxially); **leaf blades of culms** about 21 cm × 2 mm, flat with involute margins, densely scabrous adaxially. **Panicles** 8.5–13 × 4 cm, loosely contracted with approximately 75 spikelets, spikelets located at the ends of the branches, 3(4) branches on basal node, 2(3) branches in other nodes, axis and branches strongly scabrous; basal branches as long as 7 cm, more than 1/2 the length of the panicle, angled, suberect to ascending. **Spikelets** 7–9 × 3–4 mm, 5–6-flowered, broadly lanceolate, pale green; pedicels (2–) 4(–9) mm long; rachilla internodes scabrous; **glumes** lanceolate, green, margins very narrow, scarious, apex acute; **lower glumes** (5.0–)5.2–5.5(–5.7) mm long, 1-veined; **upper glumes** (6.0–)6.2–6.8(–7.0) mm long, 3-veined; **lemmas** (5.0–)5.5–6.0 mm long, 5-veined, scabrous dorsally and near apex, green, awn 1.5–2.5 mm long, scabrous; callus rounded, obliquely angled (to 45°), scabrous; **paleas** slightly shorter than lemma, bidentate at apex, keels scabrous, between keels scabrous; stamens 3, **anthers** 2.8–3.0 mm long; **ovary** densely hairy on upper 1/3. **Caryopsis** not seen.

Comments.—*Festuca molokaiensis* differs from *F. aloha* by having more delicate and thinner, more numerous and lax branches; scabrous panicles and spikelets; lemmas scabrous throughout, awns longer 1.5–2.8 mm; anthers shorter 2–3 mm; lower glumes (5.0–)5.2–5.5(–5.7) mm; and upper glumes (6.0–)6.2–6.8(–7.0) mm. In comparison to *F. aloha*, culms are scabrous on the nodes; panicles 8.5–13 cm long, more delicate, axis and peduncles scabrous, branches densely scabrous, angled; spikelets more delicate; rachilla more slender; lower glumes (5.0–)5.2–5.5(–5.7) mm long; upper glumes (6.0–)6.2–6.8(–7.0) mm long; lemmas 5–6 mm long, evenly scabrous across the back from the base to the apex, 3-veined or infrequently faintly 5-veined (lateral veins obsolete or obscure), awned, the awn 1.5–2.8 mm long; and anthers 2–3 mm long.

Etymology.—The specific epithet of *F. molokaiensis* derives from the island of Moloka'i.

Conservation status.—*Festuca molokaiensis* is only known from the type locality where it has been recorded as occasional (Oppenheimer, on herbarium label). Due to the scarcity of available data on the potential distribution, demography, and population status of *F. molokaiensis*, we consider to be a Data Deficient (DD) taxon (IUCN 2001).

TAXONOMY AND PHYLOGENY

Festuca aloha and *F. molokaiensis* are morphologically similar to the Hawaiian endemic, *F. hawaiiensis* in ligule size and shape, ovary hairiness, and leaf-blade anatomy (Hitchcock 1922). However, *F. hawaiiensis* is a more robust plant up to 150 cm tall with longer (30–40 cm) and wider panicles that are open with 3–5 spreading and drooping branches at the nodes, and larger lemmas up to 9 mm long. *Festuca hawaiiensis* grows at higher elevations, at ca. 2000 m, in rich soil on moist wooded hills on the island of Hawaii.

Festuca aloha and *F. molokaiensis* resemble the western North American, *F. californica* ssp. *hitchcockiana* (E.B. Alexeev) Darbysh. [Darbyshire & Pavlick 2007] in leaf blade cross section, panicle features, and hairy ovary apices. However, *F. californica* ssp. *hitchcockiana* differs from the new species by having a more robust and cespitose habit, possession of a continuous sclerenchyma layer on the abaxial side of the leaf blade, a partially hairy collar, and longer ligules with ciliate apices.

The new *Festuca* taxa also show similarities with Macaronesian volcanic cliff dwellers: *F. agustinii* Linding., *F. jubata* Lowe, and *F. francoi* Fern.Prieto, C.Aguiar, E. Días & M.I. Gut. (Saint-Yves 1922; Fernández Prieto et al. 2008) because all share extravaginal innovations and flat to inrolled (or conduplicate) leaf-blades with some complete sclerenchyma trabeculae. However, the latter species all differ from the new species by having glabrous ovary apices and short (< 1.5 mm) ligules.

We analyzed the ITS and *trnL-F* sequences of two samples of *Festuca aloha* from different populations from Kauai [*F. aloha* 1: Kalalau, US-3252239 (isotype), GenBank GQ162205 (ITS) and GQ162208 (trnLF) accessions; *F. aloha* 2: Pohakuao, US-3250261, GenBank GQ162206 (ITS) and GQ162209 (trnLF) accessions] and one sample of *F. molokaiensis* from the only known population from Molokai [*F. molokaiensis* 1: Kupai Gulch, BISH-728771 (holotype), GenBank GQ162207 (ITS) and GQ162210 (trnLF) accessions]. We then conducted heuristic parsimony analyses for the combined ITS and *trnL-F* dataset (10,000 random entry trees, TBR, mulpars off, saving no more than 10 trees of length <10 per replicate; 1000 bootstrap replicates with the same parameters as in the original search) using these three samples and combined them with our previous data for *Festuca* on a worldwide level (Catalán et al. 2007; Inda et al. 2008).

All three samples grouped together within the broad-leaved *Festuca* clade (Fig.3), nested within the well supported clade *Subulatae* + *Leucopoa* p.p. [92% bootstrap(BS)], which were separated from *F. californica*, *F. rubra*, and the Macaronesian *Festuca* sect. *Aulaxyper* s.l. species. *Festuca aloha* was monophyletic (99% BS) and sister to *F. molokaiensis* (98% BS).

The two *F. aloha* specimens from different populations on Kauai (*F. aloha* 1 & *F. aloha* 2) had similar sequences (99% BS; 1 *trnL-F* nucleotide substitution difference); however, the sample of *F. molokaiensis* from Molokai showed several nucleotide differences in both the ITS (five substitutions) and *trnL-F* (two substitutions) regions with respect to *F. aloha*. These molecular differences also support the taxonomic separation of the two species. Despite the limited infraspecific sampling, the ITS variation found between *F. aloha* and *F. molokaiensis*, from the same Hawaiian archipelago, is remarkable as these species show more nucleotide differentiation than that found between other closely related species [e.g. the Pyrenean *F. eskia* Ramond ex DC., and *F. gautieri* (Hack.) K. Richt. with only two ITS nucleotide substitutions], and between species from different Macaronesian archipelagos (e.g., Madeiran *F. jubata* and Azorean *F. petraea* Guthn. ex Seub. with three ITS nucleotide substitutions). Unfortunately, *F. hawaiiensis* could not be included in the molecular analysis because it is extremely rare and we have no material other than the type.

The closest relative of *F. aloha* and *F. molokaiensis* in our analyses (Fig. 3) was the eastern Asian *F. parvigluma* Steud. (88% BS), followed by the northwestern North American *F. subulata* Trin. (77% BS), both belonging to *F.* subg. *Subulatae*, and then by the Siberian–North American *F. altaica* Trin. (92% BS), placed

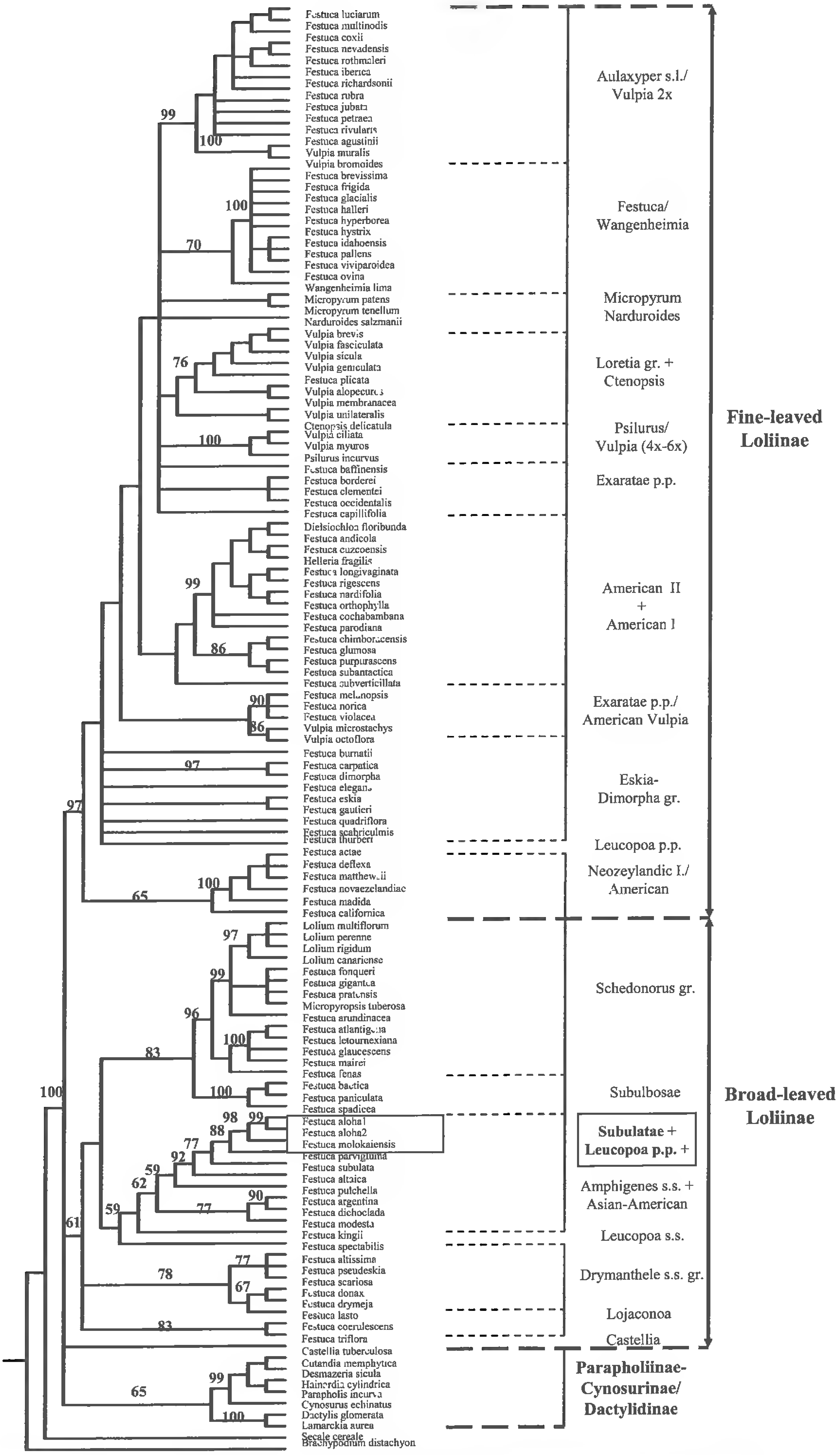

Fig. 3. Strict consensus tree of 805 most parsimonious Loliinae trees (tree length 2105; consistency index excluding uninformative characters 0.400; retention index 0.762) based on combined ITS/*trnL-F* data showing the phylogenetic placement of *Festuca aloha* Catalán, Soreng & P.M. Peterson and *F. molokaiensis* Soreng, P.M. Peterson & Catalán. Bootstrap support values are indicated on branches.

within *F.* subg. *Leucopoa* sect. *Breviaristatae*. In a separate ITS strict consensus tree the *F. aloha/F. molokaiensis* clade fell within the broad-leaved clade, and was closely related to the Asian *F. parvigluma* and *F. modesta* Steud. [sometimes treated as *Drymochloa modesta* (Nees ex Steud.) Holub]. In contrast to the ITS data, a *trnL-F* strict consensus tree placed *F. aloha/F. molokaiensis* in a polytomy at the base of the fine-leaved clade, among fine-leaved taxa and taxa intermediate between fine- and broad-leaved forms of *Festuca*.

Given the different resolutions between separate nuclear and plastid DNA sequence topologies for our species, it is possible that *F. aloha* and *F. molokaiensis* are of allopolyploid origin. On morphological grounds *F. aloha*, *F. molokaiensis*, and *F. hawaiiensis* are all part of the same complex, representing a common pattern of morphological speciation in upland habitats of different islands along the Hawaiian archipelago.

KEY TO THE SPECIES OF *FESTUCA* IN HAWAI'I

1. Lower leaf blades with auricles; leaf blades usually 5–12 mm wide, flat.
    2. Auricles ciliate on margin; lemmas awned (awn 2–3 mm), more or less scabrous distally _____ **Festuca arundinacea**
    2. Auricles not ciliate on margin; lemmas muticous, smooth or only sparsely scabrous distally _____ **Festuca pratensis**
1. All leaf blades without auricles; leaf blades 0.3–5 mm wide, involute to flat but when flat the margins involute.
    3. Ligules 0.1–0.5 mm long; ovary apices glabrous; leaf blades conduplicate; leaf sheaths usually closed below (open < ¼ their length); leaf blades of vegetative shoots in cross section without sclerenchyma girders. _____ **Festuca rubra**
    3. Ligules 1–2.5 mm long; ovary apices densely hairy; leaf blades flat with involute margins; leaf sheaths generally open ½ their length [they are fused only for 1–2 mm at the base]; leaf blades of vegetative shoots in cross section with sclerenchyma girders.
        4. Panicles 30–40 cm long, open, the branches spreading or drooping; leaf blades 3–5 mm wide ; known only from Hawaii _____ **Festuca hawaiiensis**
        4. Panicles 3.5–25 cm long, usually narrow, the branches patent, erect or ascending; leaf blades 0.3–2.4 mm wide.
            5. Lemmas scabrous only in the upper third, intermediate veins distinct, awns 0.5–1 mm long; anthers 3.1–4.2 mm long; ligules 1–1.5 mm long; lower glumes (3.6–)3.9–4.2(–4.5) mm long; upper glumes 5.2–5.5(–6.0) mm long; known only from Kaua'i _____ **Festuca aloha**
            5. Lemmas evenly scabrous throughout, intermediate veins absent or obscure, awns 1.5–2.8 mm; anthers 2–3 mm long; ligules 1.5–2.5 mm long; lower glumes (5.0–)5.2–5.5(–5.7) mm long; upper glumes (6.0–)6.2–6.8(–7.0) mm long; known only from Moloka'i _____ **Festuca molokaiensis**

ACKNOWLEDGMENTS

This work has been subsidized by the Spanish Ministry of Science and Technology Grant Project CGL2006-00319/BOS and Sabbatical Research Stay Grant PR2008-0020 to Pilar Catalán. We thank Stephen Darbyshire and Neil Snow for their critical review of an earlier version of the manuscript; Napua Harbottle, Tim Flynn, and Gerrit Davidse, for facilitating for us the study of Hawaiian *Festuca* materials deposited at BISH, PTBG and MO, respectively; Hank Oppenheimer, Neil Snow, and Cliff Morden for valuable information on the ecology and distribution of *F. aloha* and *F. molokaiensis* in Kauai'i and Molokai'i; Sasha Savytskyy, Dai Tsuchiya, and Juan Viruel for helping us with figure preparation; Alain Touwaide for correcting the Latin diagnoses; and Alice R. Tangerini for providing the illustration.

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A NEW GENUS, *MEXOTIS*, FOR FIVE MEXICAN SPECIES OF HEDYOTIDEAE (RUBIACEAE)

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ABSTRACT

In further restriction of the concept of the genus *Hedyotis* in Mexico, four known species, *H. galeottii, H. kingii, H. latifolia,* and *H. terrellii,* are placed in a new genus **Mexotis.** A new species, **M. lorencei,** is recognized and described. Morphological and distributional data are provided and representative collections are cited.

RESUMEN

En la restricción adicional en el concepto del género *Hedyotis* en México, cuatro de las especies conocidas, *H. galeottii, H. kingii, H. latifolia,* y *H. terrellii,* se colocan en el nuevo género **Mexotis.** Se reconoce una nueva especie, **M. lorencei.** Se proporcionan los datos morfológicos y de distribución y se citan las colecciones representativas.

In early 20th century literature on the tribe Hedyotideae of the Rubiaceae the name *Hedyotis* L. was applied to many members of the tribe in both hemispheres. The main recent proponent of the name *Hedyotis* was Fosberg (1943) in his treatment of 24 Polynesian species of *Hedyotis.* He stated that he was adopting *Hedyotis* in the broadest sense because "the criteria to segregate the species involve not very fundamental differences in structure" (Terrell 1996:2–5). Under *Hedyotis* he recognized five subgenera and commented that many botanists would consider these as genera. Despite his broad view of genera, he favored extreme splitting for subdivisions of species, e.g., he described 39 named forms of *Hedyotis acuminata* (Cham. & Schltdl.) Steud.(now *Kadua acuminata* Cham. & Schltdl.). He also considered seed characters as unimportant because "they vary so much that no two are alike in a single capsule". In subsequent papers Fosberg continued to use the name *Hedyotis.*

A recent study of Asian *Hedyotis* shows that many species related to the type, *Hedyotis fruticosa* L., of Sri Lanka and India, have unique capsule and seed morphology (Terrell & Robinson 2003). These species, in the genus *Hedyotis*, so far as known, are restricted to Asia and the western Pacific. Excluded from this concept are the mid-Pacific elements more recently treated as *Kadua* Cham. & Schltdl. (Terrell et al. 2005) and the New World species that have currently been placed in *Hedyotis.*

Many of the American Hedyotideae that were once placed in *Hedyotis* are now recognized as separate genera on the basis of structural features, particularly seeds and habit. Some of the segregate genera were described as new, including *Carterella*, with one Mexican species (Terrell 1987), *Stenaria* with five U.S. and Mexican species (Terrell 2001a), and *Stenotis* with seven Baja California and one Arizona species (Terrell 2001b). In addition, *Houstonia* and North American species of *Oldenlandia* each have five Mexican or Mexican-U.S. species (Terrell 1996; Terrell & Robinson 2006). In recent years further study has included about 12 additional hedyotoid genera. None of these genera were found to have seeds and other characters similar to those of the five species studied here.

We provide a further needed reclassification for Mexican *Hedyotis* species. A new genus, *Mexotis*, is described, including *Hedyotis galeottii, H. kingii, H. latifolia, H. terrellii*, and a newly described species, *M. lorencei.*

The removal of Western Hemisphere Hedyotideae from *Hedyotis* is supported by two recent studies

using DNA sequencing. In the DNA study of Andersson and Rova (1999), such species once placed in *Hedyotis* are not closely related to the Asian and eastern Pacific *Hedyotis*, the latter represented by *H. macrostegia* Stapf or the Central Pacific *H. hillebrandii* (Fosberg) Wagner & Herbst. (now *Kadua axillaris* (Wahra) Wagner & Lorence). In a more complete survey, Kårehed et al. (2008) show the division more clearly, and they call for the narrower interpretation of *Hedyotis*. Thus, the morphological and DNA evidence agree in the need to exclude American species of Hedyotideae from the genus *Hedyotis*. The Kårehed et al. study subdivides the Hedyotidae (as Spermacoceae) into many discrete clades that are not only distinct from *Hedyotis*, but distinct from each other. Two such groups are the *Arcytophyllum/Houstonia/Stenaria* Clade, to which many of the previously studied American Hedyotideae listed above belong and the *Manettia/Bouvardia* branch, the latter being close to the *Spermacoce* Clade. No DNA sequences are available for any of the species placed here in *Mexotis*, and conclusions regarding which group is closest to *Mexotis* are based on structural features.

A paper by Church (2003) contributed an important molecular study on *Houstonia* and related genera, but did not include any of the five Mexican species that we investigate here.

Mexotis includes four species of large herbs or subshrubs with woody stems, long internodes, large elliptic or ovate leaves, long petioles, filiform pedicels, and generally flattened seeds with central punctiform hila. These species are native to Oaxaca and Veracruz. A fifth smaller species, *M. latifolia*, has herbaceous or woody-based stems and smaller leaves. It appears closely related to the four more robust species and ranges from Veracruz to Guatemala. This species is the only one of the five with a known chromosome number, $n = 17$, a number not known to occur in any other species of Hedyotideae.

The five species (Table 1; Figs. 1–5) have significant reproductive and vegetative characters. The seed types fall into two groups, the kingii group and the galeottii group. The kingii group is represented by *M. kingii*, the type species, which has somewhat thicker seeds, sometimes polygonal in outline and being often obtusely angulate or obtusely ridged. The compression is moderate or slight. These exact characters have not appeared in other Hedyotideae species. *Mexotis terrellii* is also in this group because of its apparent similarity to *M. kingii*; however, unfortunately the collections have immature seeds. The second seed type group includes *M. galeottii, M. latifolia*, and *M. lorencei*. These species have thin, flat or strongly compressed, concavo-convex seeds. In *M. galeottii* and *M. latifolia* the seeds are slightly to moderately concavo-convex. In *M. lorencei* the seeds become strongly concavo-convex and may appear cupulate. In *M. galeottii* and *M. latifolia* the seed areoles (cells) are radially elongated, and *M. galeottii* is unique in having narrow, usually partial, sometimes complete, wings. These same two characters also occur in the genus *Bouvardia*, which, however, carries the winged character to extremes, as many *Bouvardia* species have broad, conspicuous wings (and large capsules) (Blackwell (1968).

Mexotis Terrell & H. Rob., gen. nov. Type species: *Mexotis kingii* (Terrell) Terrell & H. Rob.

Plantae perennes, saepe base lignosae, leniter herbaceae vel suffrutescentes. Caules ad 1.5 m alti; laminae foliorum ad 11 cm longae ovatae vel ellipticae; corollae infundibulares; semenae planatae aut leniter compressae interdum alatae, hilis centralis punctiformibus, areolis distinctis isodiametricis vel radiate elongatis.

Perennial herbs or subshrubs typically with thick, woody, erect to decumbent, stems ca. 0.4–1.5 m long, in *M. latifolia* stems 15–55 cm tall, woody only at base. Leaves opposite, blades ovate to elliptic, acute to slightly acuminate, glabrous to sparsely or minutely puberulent or pubescent. Stipules interpetiolate. Inflorescences with slender or filiform pedicels, branching alternate or partially opposite. Calyx lobes lancolate. Corollas white or purplish to rarely rose, 3–13 mm long, funnelform, valvate, 4-lobed, not appendaged, glabrous to densely pubescent inside; heterostylous, with pin and thrum forms. Capsules subglobose to broader than long, where stages are first loculicidally then septicidally dehiscent. Seeds numerous, concavo-convex or obtusely ridged, one species with narrow wing, hilum central, punctiform, areoles isodiametric or radially elongated.

The genus name, *Mexotis*, is derived from Mex- as in Mexico and –otis as in *Hedyotis*, referring to an ear.

KEY TO SPECIES OF *MEXOTIS*

1. Plants decumbent or erect, slender and only slightly woody at base, height 15–55 cm; leaf blades 4–32(–45) × 3–24 mm; calyx lobes 0.4–1.5 mm long __________ **2. M. latifolia**
1. Plants erect, with woody stems and stout woody bases, height 45–150 cm; leaf blades 25–110 × 8–40 mm; calyx lobes 1–6 mm long.
    2. Stems and inflorescence axes minutely hirtellous; seeds often obviously winged __________ **1. M. galeottii**
    2. Stems and inflorescence axes glabrous; seeds not winged.
        3. Stipules to 10 mm long; calyx lobes 5–6 mm long; capsules 5.0–5.5 × 6–7 mm __________ **5. M. lorencei**
        3. Stipules 2–4 mm long; calyx lobes 1–4.7 mm long; capsules 1–4.5 mm in diam.
            4. Inflorescences 3–15 × 6–18 cm; pedicels 7–32 long.; calyx lobes 1–2 mm long; corollas 5–6.5 mm long; stipule appendages 1–2 mm long __________ **4. M. terrellii**
            4. Inflorescences to 8 × 11 cm; pedicels 3–13 mm long; calyx lobes 1.5–4.7 mm long; corollas 7–13 mm long; stipule appendages only 0.3–0.5 mm long __________ **3. M. kingii**

1. Mexotis galeottii (M. Martens) Terrell & H. Rob., comb. nov. (**Fig. 1A–D**). *Declieuxia galeottii* M. Martens, in Martens & Galeotti, Bull. Acad. Roy. Sci. Brux. 11:231. 1844. *Hedyotis galeottii* (M. Martens) Terrell & Lorence, Phytologia 66:1–4. 1989. Type: MEXICO. Oaxaca: Llano Verde, 3–7000 ft, Apr 1840, *H. Galeotti 2603* (holotype: BR!; isotypes: BR!, US!).

Manettia liebmannii Standley, J. Washington Acad. Sci. 17:337–338. 1927. Type: MEXICO. Oaxaca: Pelado, Aug 1842, *Liebmann 11485* (holotype: C; isotype fragment: US 1315772!). Paratype: MEXICO. Oaxaca: Cuesta de San Juan del Estado, *Liebmann 11487* (C; fragment US 1315771!).

Perennial herbs or small shrubs. Stems 60–150 cm tall, to ca. 2.5 mm thick and woody toward base, stout, subterete, erect, glabrous or minutely hirtellous on upper stem and in inflorescence, few-several branched. Leaves with slender petioles 2–7 mm long, blades 40–85 ×12–38 mm, ovate or ovate-lanceolate, acuminate, glabrous above, glabrous or hirtellous on midrib beneath. Stipules 1–3 mm, broadly deltate, cuspidate with tip 1–2 mm long, glabrous or with few thick marginal teeth. Inflorescence with terminal, few-flowered cymes, branches densely and minutely hirtellous, flowers heterostylous, pedicels 2–7 mm long, very slender or filiform. Hypanthium glabrous; calyx lobes 1–2 × 0.3–0.7 mm, lanceolate, acute or submucronate, glabrous. Corollas 4.5–9.7 mm long, funnelform or broadly funnelform, white, glabrous externally; tubes 2.8–4 mm long, 1–2.5 mm wide at base, 2.2–4.5 mm wide at throat, densely puberulent within; lobes 2.2–5.2 ×1–2.5 mm, ovate, densely downy on adaxial face with white gland-tipped hairs. Pin flowers with stigma lobes 0.6–1.5 mm long, oblong or linear, exserted 1–2 mm beyond throat, anthers located at 3/4-point from base of corolla tube. Thrum flowers with anthers 1.0–1.5 mm long, linear or narrowly oblong, sessile or on filaments 0.5 mm long, attached at sinuses, stigmas located at midpoint of corolla tube. Capsules 2.2–4.0 × 2.2–4.5 mm, subglobose or somewhat compressed, 3/4–4/5 inferior, rather thick-walled, glabrous, loculicidally dehiscent. Seeds 0.8–1.2 × 0.8–1.2 mm, black, strongly compressed, very thin, flat, slightly to moderately concavo-convex, in outline orbicular or suborbicular, margins thin, wings present or absent, complete or partial, very narrow, 0.1–0.2 mm wide, fragile, hilum punctiform, testa finely reticulate, areoles radially elongated (Fig. 1). The pollen was found by Joan Nowicke (Terrell et al. 1986) to be similar to that of *Hedyotis kingii*. Chromosome number unknown.

Distribution and Habitats.—Forests and rocky slopes. México: Oaxaca. Llano Verde area, Sierra de Juarez, north of the city of Oaxaca; Veracruz, in Sierra Madre Oriental northeast and northwest of Xalapa.

Notes.—Additional nomenclatural and morphological notes were included in the Terrell and Lorence (1989) description of *Hedyotis galeottii*. The minute pubescence on the stems and inflorescence branches distinguish the species.

Additional specimens. Labelled *Hedyotis liebmannii* (see nomenclature above) and cited here based on data from D. H. Lorence. **MEXICO. Veracruz:** Mpio. Alto Lucero, El Cerro la Cima, entre Plan de las Hayas y Tierra Blanca, 1600m, *Castillo C. & Narave 2158* (XAL); Mpio. Atzalan, Cerro del Aguila, 850 m, 10 Sep 1982, *Ventura A. 19740* (ENCB); Mpio. Atzalan, Alseseca, 950 m, 24 Mar 1975, *Ventura A. 11118* (ENCB); Mpio. Atzalan, La Calavera, 1000m, 27 Apr 1978, *Ventura A. 15232* (ENCB); Mpio. Naolinco, Naranjillo, 1250 m, 13 Nov 1976, *Ventura A. 13605* (ENCB); Mpio. Yecuatla, Santa Rita, 1450 m, 12 Feb 1973, *Ventura A. 7824* (ENCB); Mpio. Yecuatla, Loma Santa Rita, 1480 m, 12 Jan 1972, *Ventura A. 4764* (ENCB). **Oaxaca:** Yolox Rancho Grande, al oesta de Cuasimulca, *Miranda 1094* (MEXU).

2. Mexotis latifolia (M. Martens & Galeotti) Terrell & H. Rob., comb. nov. (**Fig. 1E, F**). *Oldenlandia latifolia* M.

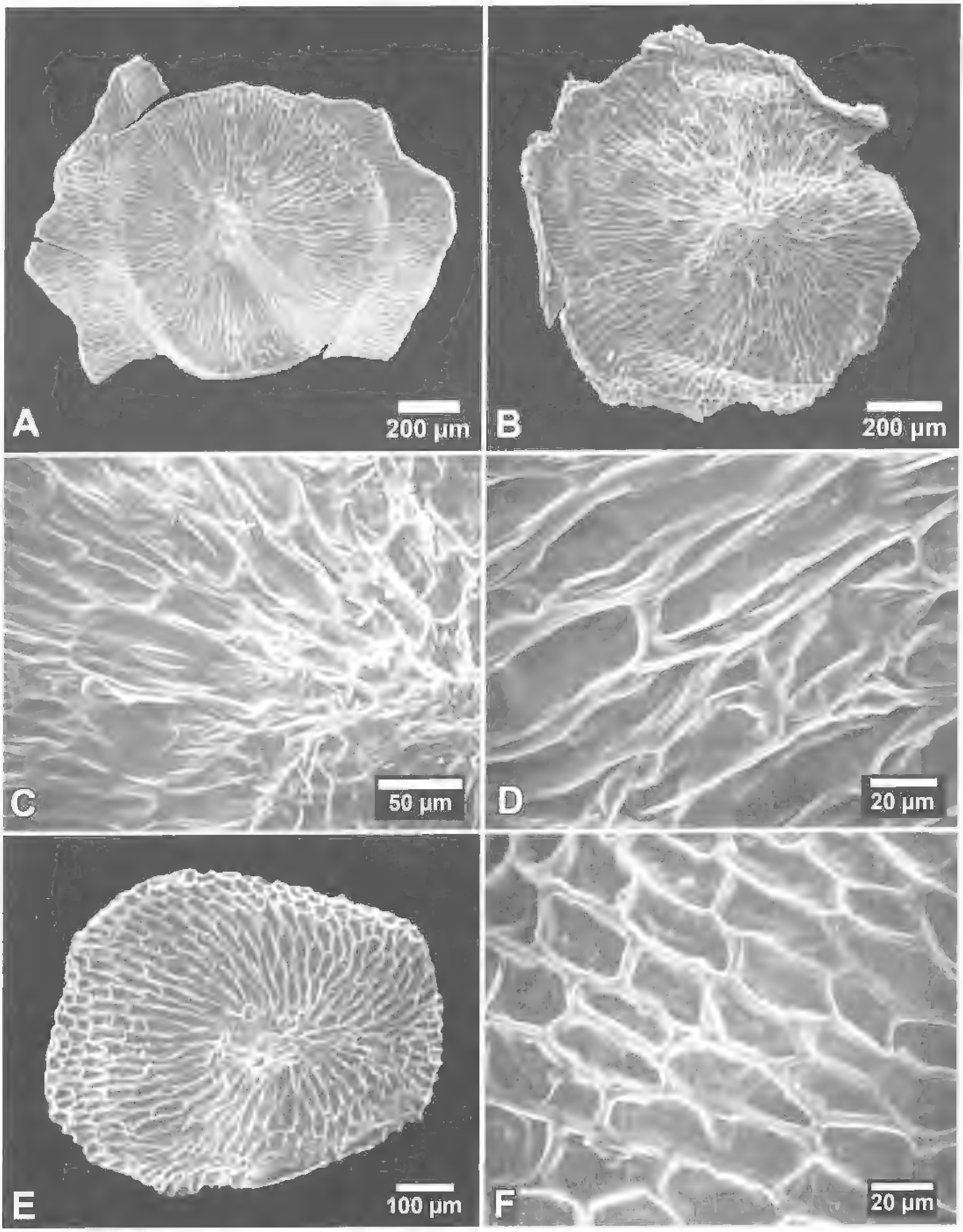

Fig. 1. Seeds examined by SEM. A–D. *Mexotis galeottii*. A. *Castillo C. & Narave 2158* (XAL) Verucruz. B–D. *Ventura A. 11118* (ENCB), Veracruz. E, F. *Mexotis latifolia*. *Purpus 2951* (NY), Veracruz. A, B, E. Seeds, ventral views, flat, with/without wings. C. Areoles rectangular, radially elongated, showing hilum. D, F. Areoles enlarged.

Martens & Galeotti, Bull. Acad. Roy. Sci. Brux. 11:235. 1844. Hedyotis latifolia (M. Martens & Galeotti) Walp., Rep. 6:55. 1846. Type: MEXICO. Veracruz: Mirador, at 3000 ft, near Jalapa, May 1840, Galeotti 2556 (holotype: BR; isotypes: F! GH! K!).

Hedyotis dichotoma Sessé & Moc., Fl. Mexic. ed.2. 20.1893, non H. dichotoma Cav., Icon. 6:53. 1801. Type: Sessé, Mociño, Castillo, & Maldonado 556 (isotype: F!).

Houstonia gracilis Brandegee, Zoe 5:238. 1907, non Hedyotis gracilis DC., Prodr. 4:419. 1830. Type: MÉXICO. Veracruz: on rocks near Orizaba, May 1905, C.A. Purpus 1251 (lectotype: UC! isolectotypes: F! MO!).

Hedyotis exigula W.H. Lewis, Rhodora 63:221. 1961. New name.

Perennial herbs with roots sometimes woody. Stems 15–55 cm tall, occasionally rather woody at base, tetragonal or rounded-tetragonal, slender, erect, decumbent or spreading, glabrous or rarely pubescent, sparsely to much branched. Leaves with petioles to ca.10 mm long, blades 4–32(–45) × 3–14(–24) mm, median blades ovate to broadly elliptic or ovate-lanceolate, upper blades becoming lanceolate or linear-lanceolate, glabrous or puberulent above, glabrous beneath, base rounded to cuneate, apex obtuse or rather acute. Stipules to 2 mm long and wide, ovate or deltate, glabrous or short-pubescent, margin with several glandular teeth to ca. 1.5 mm long, apices truncate to lacerate. Inflorescence with terminal, few-flowered cymes, flowers heterostylous, closed at night, pedicels to 5(–10) mm long, very slender or filiform. Hypanthium glabrous or puberulent; calyx lobes 0.4–1.5 × 0.2–0.7 mm, scarcely to somewhat longer than capsules, erect, deltate to lanceolate, apices acute or obtuse, margins and sinuses glabrous or with white hairs to ca. 0.1 mm long. Corollas 3–7.3 mm long, funnelform or broadly funnelform, white, purplish, or rarely rose, glabrous externally; tube (2–)2.3–3.3(–4) mm long, usually 1–2 times longer than lobes, somewhat widened distally, 0.6–1.4 mm wide at base, 1.8–3 mm wide at throat, glabrous or puberulent within; lobes 1–3.3 × 0.6–2 mm, ovate, glabrous or puberulent within. Pin flowers with stigma lobes 0.4–1.3 mm long, linear, exserted 0.5–2 mm beyond corolla throat, style 2.4–4.3 mm long, filiform, anthers 0.5–0.8 mm long, 0.2 mm wide, narrowly oblong or elliptic, yellow or whitish, included near midpoint of corolla tube, sessile or subsessile. Thrum flowers with anthers 0.7–1.2 × 0.2–0.3 mm, narrowly elliptic or narrowly oblong, yellow or whitish, exserted at throat on filaments 0.2–0.8 mm long, stigma lobes 0.4–0.6 mm long, included near midpoint of corolla tube on style 1–1.6 mm long, filiform. Capsules 1–2.7 × 1–3.5 mm, usually slightly wider than long, or subequal, usually 3/4 to 9/10 inferior, moderately compressed, thin-walled, glabrous or with few hairs on calyx margins, cuneate or rounded toward base, apex retuse, dehiscing widely loculicidally and then septicidally. Seeds 8–24 per capsule, 0.5–1 × 0.4–0.9 mm, black, strongly compressed, very thin, slightly to moderately concavo-convex, in outline broadly elliptic to suborbicular, margins thin or slightly rounded, hilum punctiform, testa finely reticulate, areoles radially elongated (Fig. 1). Chromosome number: n = 17 (Lewis in Terrell et al. 1986, as Houstonia gracilis).

Phenology.—Flowering throughout year.

Distribution and Habitats.—Moist soil, shaded places, banks, slopes, among rocks, sides and bases of cliffs, montane rain forest; altitudes recorded for a few collections vary from 330–1430 m (1000–4300 ft). Mexico: Veracruz (mainly from Cofre de Perote and Jalapa south to Orizaba), northern Oaxaca, Chiapas, and west and central Guatemala.

Notes.—Stephen Koch reported (pers. comm. 1980) that this species was for sale in Coyoacan, Mexico City, as a house plant. It grows rapidly and continually produces numerous small flowers.

Standley (1918) listed Oldenlandia latifolia as a synonym of O. microtheca DC., but the type of O. latifolia (see above) has flat seeds and reticulate testas, as opposed to O. microtheca (Schltdl. & Cham.) DC. which has angular seeds with the areole walls coalescent. The basionym O. latifolia thus supplants the previously accepted names, Hedyotis exigula and Houstonia gracilis.

A paper on Oldenlandia (Terrell & Robinson 2006) provided a key to Oldenlandia microtheca and Hedyotis latifolia (Mexotis latifolia), two superficially similar species differing by seed characters and chromosome numbers (the former n = 11. latter n = 17).

Mexiotis latifolia is a variable species. Its relationships to the other four species in Mexiotis remain to be determined. It resembles Houstonia purpurea L. of eastern U.S. in aspect and leaf shape and size, but differs in seeds and reproductive characters.

Representative specimens: **MEXICO. Chiapas:** Lagos de Montebello, 42 km NE of La Triniteria, 23 Oct 1971, *Breedlove & Thorne 21112* (DS, MICH, MO). **Veracruz:** mpio. Ixtaczoquitlan, Parque de Cerveceria Moctezuma, 1 km SE of Fortin, 970 m, 9 Nov 1978, *Koch & Fryxell 78185* (CHAPA, ENCB, XAL); Cerro de Chicahuaxtla-Cuauhtlapan, 22 Jan 1968, *Marino Rosas R. 1034* (CAS, MO); Mt. Orizaba, *Seaton 101* (F, GH, K, NY, US); near Rio Blanco and Orizaba, 4300 ft, 15 Sep 1944, *Sharp 44889* (GH, MEXU, TENN, US); side road between Orizaba and Fortin, 3200 ft, 23 May 1973 *Terrell & King 4450*, (US); Tepejilotla, mpio. Chocaman, 29 Jun 1979, *Ventura A. 16282* (ARIZ, CHAPA, ENCB, MO). **GUATEMALA. Huehuetenango:** 5 mi SE of Barillas, Sierra de los Cuchumatanes, 1150 m, *Steyermark 49537* (GH).

3. Mexotis kingii (Terrell) Terrell & H. Rob., comb. nov. (**Figs. 2, 3**). *Houstonia kingii* Terrell, Brittonia 32:491. 1980. *Hedyotis kingii* (Terrell) G.L. Nesom, Syst. Bot. 13:434. 1988. Type: MEXICO. Oaxaca: E-facing slopes, mountains along rt. 175, 28 km by road S of Valle Nacional on way to Ixtlan de Juarez; rain forest abounding in ferns, bromeliads, orchids, and aroids; elev. ca. 2000 m; not common; full sun; gravelly soil, 30 Jul 1959, *R.M. King 2107* (holotype: MICH!, 2 sheets, one flowering, one fruiting).

Perennial herbs with thick, woody roots. Stems to 45 cm tall, to ca. 5 mm thick and somewhat woody toward base, tan or straw-colored, subterete, rather stout, erect, glabrous, branched. Leaves with petioles to 10 mm long, blades 40–85 × 8–30 mm, elliptic, ovate, or lanceolate-ovate, acuminate, glabrous, slightly paler beneath. Stipules to 2 mm long, broadly rounded, lobed, the central lobe with recurved glandular hairs. Inflorescence in terminal, few-flowered cymes, widely branching, to 8 × 11 cm, flowers heterostylous, pedicels to 13 mm long, very slender or filiform. Hypanthium glabrous; calyx lobes 1.5–4.7 × 0.3–0.8 mm, 1/2–3/4 as long as corolla tube, linear or narrowly lanceolate, acute or acicular, sometimes divaricately spreading. Corollas 7–13 mm long, broadly funnelform, white or light purple, glabrous externally; tube 3–9 mm, 3–7 mm wide at throat, glabrous or puberulent within; lobes 2.5–7.0 × 1.5–3.3 mm wide, shorter than to slightly longer than the tube, ovate, glabrous or puberulent within. Pin flowers with stigma lobes 0.5–1.3 mm long, narrowly oblong or linear, near corolla throat or slightly exserted, anthers located at 1/3–1/4-point from base of corolla tube. Thrum flowers with anthers 1.3–2.0 mm long, narrowly oblong, purple, attached at corolla throat, subsessile or filaments to 1.5 mm long, stigmas located at 1/4–point from base to midpoint of corolla tube. Capsules (only previous year's dehisced capsules seen) 3–4 × 3–4 mm, subglobose, thin-walled, glabrous, 3/4–7/8 inferior. Seeds 0.6–1.1 × 0.5–0.9 mm, dark brown, moderately to slightly compressed, often polygonal in outline, obtusely angulate or obtusely ridged, margins rounded, hilum punctiform, testa finely reticulate, areoles small, isodiametric. Pollen illustrated in Terrell et al. 1986, figs 21, 22. Plant and seeds illustrated here in Figures 2, 3. Chromosome number unknown.

Phenology.—Flowering December to July.

Distribution.—México: Oaxaca. Original collection in a cloud forest of the Sierra Juarez range along or near highway 175 from Ixtlán de Juarez to Valle Nacional, 28 km south of Valle Nacional. Additional occurrences in Oaxaca cited below are mostly along hwy. 175 between Tuxtepec and Oaxaca city; the location of Tarabunde is unknown. On 22 July 1987 Stephen Koch and Terrell, somewhat hampered by a torrential rain, searched unsuccessfully for the species along Highway 175.

Additional specimens examined. **MEXICO. Oaxaca:** Distr. de Ixtlan, roadside, trop. vegetation with tree ferns, 24 mi S of Valle Nacional, Hwy. 175, 22 Mar 1978, *Poole et al. 1283* (LL); bosque mesofilo perturbado, 1750 m, 38 km S of Valle Nacional, 11 Apr 1976, *Rzedowski 34092* (ENCB); km 128 entre Llano de Las lores y Tuxtepec, 26 Dec 1965, *Delgadillo 121* (MEXU), reported by Lorence; Mpio. de Comaltepec, Hwy. 175, "Vista hermosa," selva secundaria, km 137, 1500 m, 11 May 1966, *Martinez Calderon 801* (ENCB, MEXU, XAL); Tarabunde, 7 Feb 1966, *MacDougal 17* (US); 22–26 mi S from Valle Nacional on Hwy. 175, cloud forest, 7 Jan 1989, *Todzia et al. 2839* (TEX).

4. Mexotis terrellii (Lorence) Terrell & H. Rob., comb. nov. *Hedyotis terrellii* Lorence, Novon 7:51.1997. Type: MÉXICO. Oaxaca: Distrito de Mixe, Municipio de Totontepec, 3 km al SO de Totontepec, carretera a Mitla, 1910 m, bosque mesófilo, 6 Sep 1986, *R. Torres C. & C. Martinez 9067* (holotype: PTBG 12314; isotype: MEXU).

The following description is modified from that of David Lorence (1997). Perennial herbs. Stems 45–80 cm tall, branching from the base with several erect stems 2.0–3.5 mm diam. and somewhat woody toward base, terete, glabrous. Leaves with petioles 3.5–5 mm long, blades (25–)45–100 × 10–40 mm, elliptic to ovate-elliptic, the base often decurrent, apex acuminate, glabrous, chartaceous, margins sometimes with few small teeth. Stipule body to 4 mm long, truncate or deltate, with apical and lateral linear gland-tipped teeth 1–3

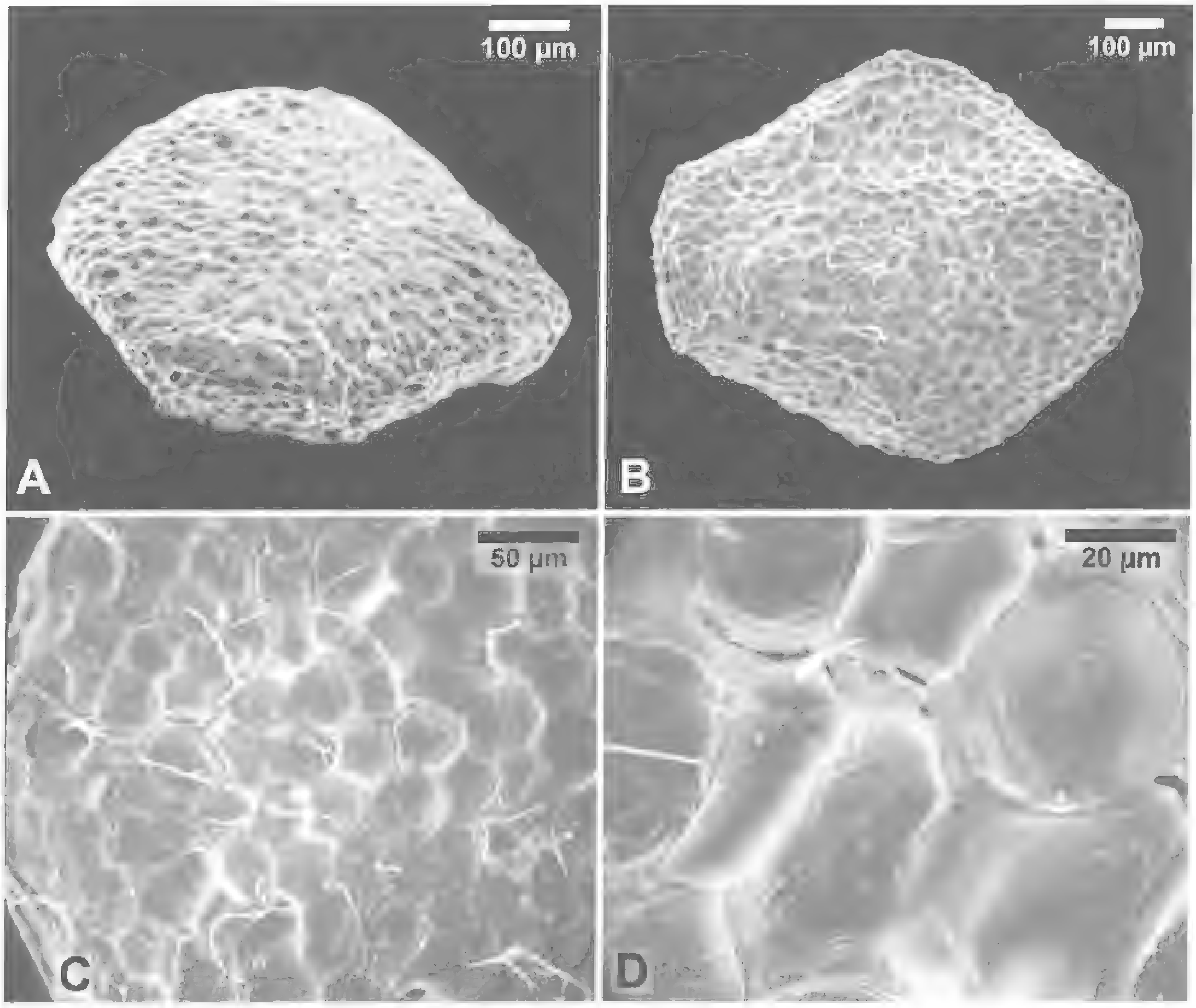

Fig. 2. Seeds of holotype of *Mexotis kingii* examined by SEM. A, B. Seeds polygonal, flat, slightly or somewhat thickened. C, D. Areoles mostly polygonal, not radially elongated.

mm long. Inflorescences terminal, compound cymes 3–15 × 6–18 cm, subtended by reduced leaves, branching dichasially to 2° or 3°, the primary branches 2–5 cm long, the axes slender, glabrous, subtended by stipule-like bracts, flowers on filiform pedicels 7–32 mm long. Hypanthium broadly obconic, glabrous. Calyx lobes 1–2 × 1–2 mm, deltate, glabrous. Corolla in bud quadrangular, rounded at apex, at anthesis 5–6.5 mm long; tube 2–2.5 mm long glabrous, lobes 3–4 mm long, erect or slightly spreading, elliptic, acute at apex, externally glabrous, internally villosulous with crinkled, white trichomes. Stamens attached near middle of tube below sinuses, the filaments 0.5 mm long, anthers 1 mm long, linear-elliptic, style 2–2.5 mm. Stigma lobes 1 mm long, linear. Capsules 2–3 × 3–4 mm, slightly wider than long, 1/2 inferior, thin-walled. Seeds immature. Plant illustrated in Lorence 1997.

Phenology.—Collected in flower in March, and in flower and fruit in June and September.

Distribution.—Known only from the area around the type locality in cloud forest at ca. 1900 m. near Totontepec in the mountainous Mixe District of Oaxaca.

Notes.—Lorence (1997) compared certain characters of *M. terrellii* with those of *M. galeottii* and *M. kingii*. *Mexotis terrellii* particularly resembles *M. kingii*, as summarized in Table 1.

Additional specimens examined. Paratypes: **MEXICO. Oaxaca:** Distrito Ixtlán, Llano Verde, collector unknown, *Herb. Reichenbach fils III-396*(W); Distrito Mixe, mpio. Totontepec, Totontepec, bosque mesófilo de montaña, 1900 m, 17°15'N, 96°02'W, 11 Mar 1990, *Rivera R. &*

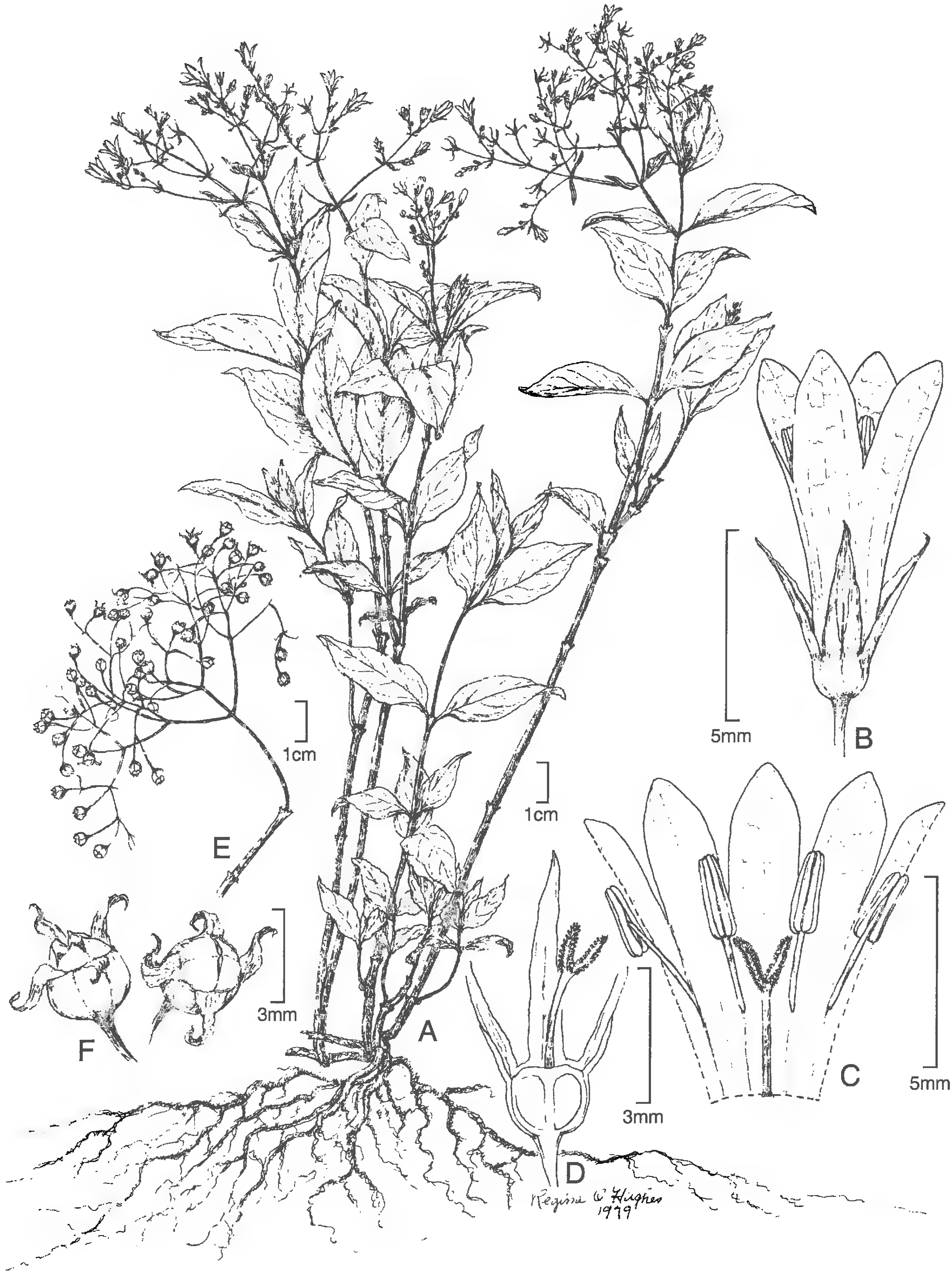

Fig. 3. *Mexotis kingii*, holotype. A. Habit. B. Flower. C. Corolla with stamens, style, and stigma. D. Ovary sectioned, with calyx lobes and stigmas. E. Inflorescence fruiting. F. Mature capsules. Drawing by the late Regina O. Hughes from Brittonia 32:492. 1980.

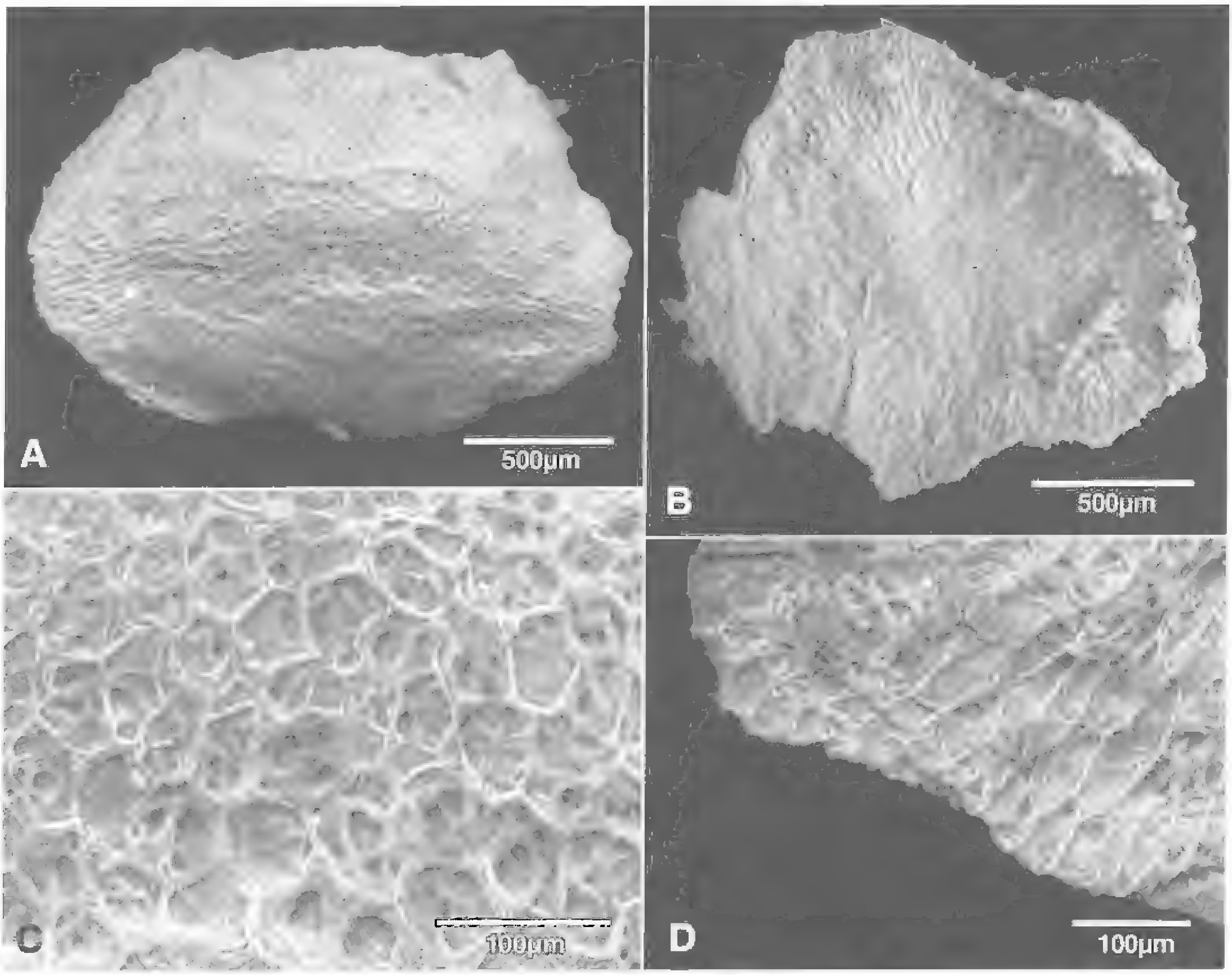

Fig. 4. Seeds of holotype of *Mexotis lorencei* examined by SEM. A. Dorsal convex surface. B. Ventral concave surface with narrow wing-like margin. C. Areoles, dorsal surface, isodiametric. D. Areoles, ventral surface, somewhat radially elongated.

Martin 1403 (PTBG, UC); Distrito Mixe, mpio.Totontopec, 2 km al SO de Totontepec, carretera a Oaxaca, 1900 m, 17 Jun. 1986, *Torres C & Téllez 8643* (MEXU, PTBG).

5. Mexotis lorencei Terrell & H. Rob., sp. nov. (**Figs. 4, 5**). Type: MEXICO. Oaxaca: Bosque de pino-encino perturbado, Distr. Santiago Juxtlahuaca, Mpio. San Martin Peras, 1 km de la desviaciaón del poblado de Escopeta, km 24 carretera San Sebastián Tecomoxtlahuaca, Lat. 17.17 N. Long. 98.09 W., Alt. 2655 m, 29 Nov 1994, *J.I. Calzada 19568* (holotype: MEXU; isotype: PTBG).

Ad *Mexotida kingii* et *M. terrellii* simila sed in stipulis et lobis calycis et capsulis majoribus distincta.

This description is based only on one large branch in fruiting condition. Perennial herb to 80 cm tall. Stems 8 mm or more thick, widely branched. Leaves with slender petioles 10–25 mm long, blades 70–110 x 13–30 mm, elliptic or ovate-lanceolate, acuminate. Stipule body to ca. 5 mm long, with several linear apical and lateral gland-tipped teeth to 10 mm long. Inflorescence in fruiting condition only, pedicels to ca. 15 mm long, slender. Calyx lobes ca. 5–6 mm long, linear or narrowly lanceolate. Corollas lacking. Capsules mature, 5–5.5 x 6–7 mm, distinctly wider than long. Seeds (only a few available) 1.4–1.8 x 1.4–1.8 mm, dark brown, orbicular or broadly elliptic in outline, thin, strongly (cupulate) to moderately concave-convex, hilum punctiform, testa reticulate, areoles not clearly visible. Fig. 5.

Distribution and habitats.—The collection label stated "Negro con calizas," which we suppose referred to black soil with limestone or limey soil. The locality was in a disturbed pine-oak forest on the west side of Oaxaca not far from the Guerrero border. This area is roughly 100 miles or 160 km from the other species and we have not seen any related collections from this part of Oaxaca.

FIG. 5. *Mexotis lorencei, J.I. Calzada 19568,* isotype (PTBG).

TABLE 1. Morphological characters of five species in genus *Mexotis*.

	M. galeottii	*M. latifolia*	*M. kingii*	*M. terrellii*	*M. lorencei*
Stems height cm	60–150	15–55	to 45	45–80	to 80
Leaf blades L × W mm	40–85 × 12–38	4–32(–45) × 3–24	40–85 × 8–30	25–100 × 10–40	70–110 × 13–30
Inflor. L × W cm	3.5 × 2.5–5	no data	to 8 × 11	3–15 × 6–18	no data
pedicel L mm	2–7	to 5(–10)	3–13	7–32	to 15
vesture	hirtellous	glabrous	glabrous	glabrous	glabrous
Calyx lobes L mm	1–2	0.4–1.5	1.5–4.7	1–2	5–6
Corollas L mm	4.5–9.7	3–7.3	7–13	5–6.5	no data
tubes L	2.8–4	2–4	3–9	2–2.5	
inner vesture	villous	glab./puberulent	glab./puberulent	glabrous	
lobes L	2.2–5.2	1–3.3	2.5–7.0	3–4	
Capsules L × W mm	2.2–4.0 × 2.2–4.5	1–2.7 × 1–3.5	3–4 × 3–4	2–3 × 3–4	5–5.5 × 6–7
Seeds L × W mm	0.8–1.2 × 0.8–1.2	0.5–1.0 × 0.4–0.9	0.6–1.1 × 0.5–0.9	immature; no data	1.4–1.8 × 1.4–1.8

Notes.—We name this species for David Lorence, who called our attention to the Calzada collection and who has contributed much to knowledge of Rubiaceae in Mexico.

This species resembles the other three species with stout woody stems and large leaves. Although only one collection is known, there are capsule, seed and stipule characters for consideration. The capsules and seeds are distinctly larger than in other species. The seeds have a thin, strongly (cupulate) to moderately concavo-convex body. Other species in this genus have flat or slightly concavo-convex seeds.

ACKNOWLEDGMENTS

David Lorence provided loans and important data on *Mexotis galeottii*, *M. terrellii*, and *M. lorencei*. In earlier times Stephen Koch provided very helpful field assistance. We thank Scott Whittaker, Electron Microscope Laboratory, Smithsonian Institution, for the SEM illustrations, and Marjorie Knowles and Alice Tangerini for preparing the figures. David Lorence and Warren Wagner are thanked for providing in-depth reviews of the manuscript. The curators of the cited herbaria helpfully provided Terrell with loans during a number of years long past.

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CAPSICOPHYSALIS: A NEW GENUS OF SOLANACEAE (PHYSALEAE) FROM MEXICO AND CENTRAL AMERICA

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ABSTRACT

A new genus from the highlands of eastern and southern Mexico and Central America is described. **Capsicophysalis** is based upon *Chamaesaracha potosina*, first described from San Luis Potosi, Mexico. *Athenaea cernua*, first described from Guatemala, is placed in synonymy. The genus has an unequally 5-lobed corolla, red fruit, 5-lobed, reflexed fruiting calyx (at maturity) and seeds with a tuberculate testa, features unknown in related genera of Solanaceae. A comparative table giving the distinguishing features of *Capsicophysalis* and *Chamaesaracha* is provided.

RESUMEN

Se describe un nuevo género que se distribuye en las montañas del este y sur de México, así como en Centro América. **Capsicophysalis** está basado en *Chamaesaracha potosina*, descrita de San Luis Potosí, México. *Athenaea cernua*, descrita originalmente de Guatemala y que ha sido transferida a tres géneros, queda como sinónimo. El nuevo género tiene una corola irregularmente 5-lobulada, fruto rojo, un cáliz 5-lobulado reflejo al madurar, y semillas con una testa tuberculada. Todas estas características se desconocen en otros géneros relacionados de las solanáceas. Se incluye un cuadro comparativo que permite diferenciar *Capsicophysalis* de *Chamaesaracha*.

KEY WORDS: Solanaceae, *Athenaea*, *Chamaesaracha*, *Physalis*, *Physaleae*, *Physalineae*, Guatemala, Mexico

Hunziker (2001) recognized section *Capsicophysalis* within *Chamaesaracha*, a genus of about 10 species distributed in the arid regions of the southwestern United States and adjacent northern Mexico. Within the section he included three species: *C. cernua*, *C. potosina*, and *C. rzedowskiana*. Hunziker listed *C. cernua* as the type species of the section. All of the species are relatively rare. Hunziker (1980) noted that only seven collections of *C. cernua* were known. We add an additional 7 for a total of 14. Until this study *C. potosina* has been known only from the type collection, all other specimens having been referred to *C. cernua* (= *Athenaea cernua*). Only two collections of *C. rzedowskiana* are known to us, both of which are from San Luis Potosi, Mexico.

Chamaesaracha cernua also has been included in *Physalis* and *Athenaea* and is treated as *Athenaea cernua* in most recent literature. Waterfall (1967) treated the taxon as a variety of *Physalis melanocystis* (Robins.) Bitter. More recently, Hunziker (1980) agreed with Gentry (1973) that the treatment of this species in *Physalis* was unacceptable and, in addition, made a very strong argument for its exclusion from *Athenaea*, which, as now conceived, is a small Brazilian genus of about ten woody species.

Careful morphological comparisons indicate that *C. cernua* and *C. potosina* are conspecific with *potosina* the oldest specific epithet. The species differs in a number of critical features from *Chamaesaracha*, *Physalis*, and *Athenaea*, and is best treated within a new and separate genus, *Capsicophysalis*. *Chamaesaracha rzedowskiana* differs from *Capsicophysalis* in distribution, flowers, fruit and fruiting calyx and, for now, is retained in *Chamaesaracha*.

Chamaesaracha and *Capsicophysalis* (as *Chamaesaracha cernua*) were included by Estrada and Martínez (1999) in their morphology based cladistic analysis of *Physalis* and related genera. They concluded that *C, potosina* was not closely related to either *Physalis* or *Chamaesaracha*. In the strict consensus tree, *C. potosina* forms a clade with *Leucophysalis viscosa* which Averett (2009a) now recognizes as a distinct genus, *Schraderanthus*. *C. potosina* further differs from *Chamaesaracha* in that it is an annual herb of mesic riparian forests (Table 1).

Capsicophysalis potosina is relatively rare and is represented by only a few collections in herbaria. Unfortunately, mature fruiting calyces are not always seen and the feature has not been noted in the literature. However, it clearly is present on a number of specimens, including type material of both *C. potosina* and *C. cernua*. The very distinctive irregularly lobed corolla, once seen, is easily observed on herbarium sheets but has not been noted in the literature. The mature calyx also appears to be a dark red on herbarium sheets. More information on these interesting characters would be welcome.

Capsicophysalis (Bitter) Averett & M. Martínez, stat. nov. *Physalis* sect. *Capsicophysalis* Bitter. Repert. Spec. Nov. Regni Veg. 20:370. 1924. *Chamaesaracha* sect. *Capsicophysalis* (Bitter) Hunz., Genera Solanacearum 230. 2001. Type species, *Capsicophysalis potosina* (B.L. Rob. & Greenm.) Averett & M. Martínez.

Annual or weak perennial herbs to 1 m high; herbage glandular pubescent, mixed with longer hairs; leaves petiolate, thin to membranous; flowers 1–2 in axils, campanulate–subrotate, 1.5–3 cm wide, corolla white, yellowish, or yellow-green with villous pads in the throat, unequally 5-lobed and slightly irregular, aestivation plicate; calyx campanulate, 5-lobed, accrescent in fruit, at first loosely investing the berry, then splitting and becoming reflexed below the berry, red, the lobes thickened along the margins; fruit a berry, shiny red or orange-red; seeds discoid 1–1.5 mm long, testa tuberculate.

The striking features of this distinctive genus include the irregular corolla, red or orange-red fruit, the red reflexed, deeply lobed structure of the mature calyx, and rod-like projections on the seed testa (Fig. 1). All of these features are uncommon among related genera, and the irregular corolla is completely novel. The latter character is evident in the types of both *C. potosina* and *C. cernua* and present in all of the cited specimens with flowers. The red fruit is largely unknown among potential relatives except in *Brachistus* and *Schraderanthus viscosus*, both of which have 6–8(–10) flowers arising in fascicles from the axils and other distinguishing features.

Capsicophysalis potosina (B.L. Rob. & Greenm.) Averett & M. Martínez, comb. nov. (**Figs. 1–2**). Basionym, *Chamaesaracha potosina* B.L. Rob. & Greenm. Amer. J. Sci. 50:161. 1895. *Saracha potosina* (B.L. Rob. & Greenm.) Averett, Ann. Missouri Bot. Gard. 57:380. 1971. Type: MEXICO. San Luis Potosi: Tamasopo Canyon, Nov 1880, *Pringle 3654* (holotype: VT!; isotype: GH!).

Athenaea cernua Donnell Smith, Bot. Gaz. 48:297. 1909. *Physalis melanocystis* (Robins.) Bitter var. *cernua* (Donnell Smith) Waterfall, Rhodora 69:99. 1967. *Chamaesaracha cernua* (Donn.-Sm.) Hunz., Contr. Gray Herb. 210:25–26. 1980. Type: GUATEMALA. Dept. Alta Verapaz: Sasia, 900 m, May 1908, *Tuerckheim II 2245* (holotype: US!; isotype: CORD).

Physalis capsicoides Bitter, Repert. Spec. Nov. Regni Veg. 20:371. 1924. Type: MEXICO. Veracruz: Papantla, Jan 1829, *Schiede 1191*. *Note*.—Hunziker (1980) notes that he has not seen any material of this collection but the long and precise description agrees in detail with the taxon in question. We also have not seen material of this collection.

Plants herbaceous annuals or weak perennials to 1 m high; herbage largely glabrous except for a few hairs along the stems and leaf margins; leaves petiolate, blades 2–4 cm long and 1–2 cm wide (about ½ as wide as long), narrowly ovate-lanceolate, margins entire, acute-acuminate at the tip, lamina thin, on short petioles; flowers 1–2 from axils on pedicels 3 cm long, flowering calyx ca 15 mm long and 12 mm wide, campanulate and rounded at the base, divided 1/2–3/4 its length, lobes acute to slightly acuminate; corolla ca. 1 cm long, yellow-white, rotate-campanulate; anthers white-yellow, 2 mm long, filaments ca 3 mm long, connected to the base of the anthers; fruiting calyx 8–12 mm long and wide, campanulate, exceeding the berry and becoming reflexed at maturity, berry orange-red to bright red at maturity; seeds dark brown, testa tuberculate with rod-like projections.

Distribution.—*Chamaesaracha potosina* is distributed from Guerrero and Tamaulipas in Mexico south to Guatemala and Honduras (Fig. 2).

Additional material examined: **BELIZE. Cayo:** Arenal-Valentine road, Jun–Aug 1936, *Lundell 6181* (US); Vaca Plateau, 8 Mar 1980, *Whitefoord 2023* (MO). **GUATEMALA. Peten:** Dolores, 22 Aug 1961, *Contreras 2746* (LL); Dolores, 5 km E of village, 30 Aug 1961, *Contreras 2830A* (TEX); Tikal, 18 Jan 1962, *Lundell 17186* (LL); Tikal Nat'l. Park, 14 Feb 1959, *Lundell 15548* (LL); Tikal Nat'l. Park, 9 Mar 1959, *Lundell 15805* (LL); Ciebal, Sayaxche, 17 Mar 1970, *Contreras 9764* (LL). **HONDURAS. Dist. Toledo:** Edwards road beyond Columbia, 15 May 1948, *Gentle 6535* (LL). **MEXICO. Chiapas:** 9 km S de Palenque, 6 Apr 1985, *Cabrera & Cabrera 8168* (TEX); Mpio. Ococingo, 14 Sep 1985 *Martínez 13823* (TEX). **Guerrero:** Montes de Oca, 21 April 1938, *Hinton 14034* (GH, LL); Dist. Galena, Carrizo-El Río, 20 Oct 1939, *Hinton 14689* (GH). **Oaxaca:** Mpio. Sta. Maria Chimalapa, 26 July 1985, *H. Hernandez G. 1375* (TEX). **Tamaulipas:**

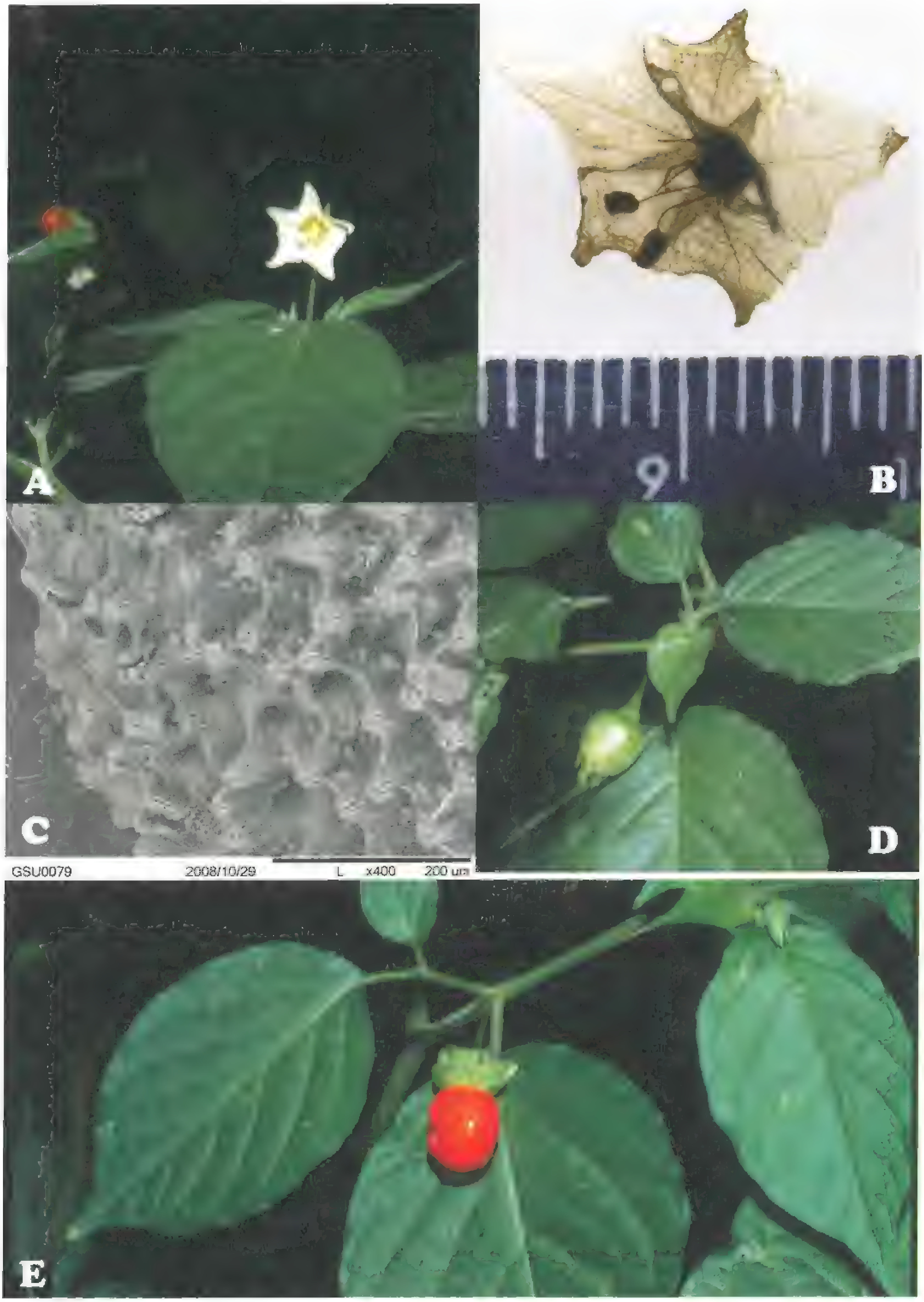

Fig. 1. *Capsicophysalis potosina*: **A.** flower; **B.** cleared flower showing unequal lobes; **C.** SEM of seed; **D.** immature fruit with calyx enclosing the berry; **E.** mature fruit with red berry and reflexed calyx.

Fig. 2. Distribution of *Capsicophysalis potosina*.

Mpio. Victoria, Cañon de La Libertad, May 1994, *Martínez s.n.* (UAT); Mpio. de San Nicolás, a 5 km del inicio de la brecha a González, 28 Nov 1998, *Martínez 5329* (QMEX).

GENERIC RELATIONSHIPS

Capsicophysalis probably is most closely related to *Schraderanthus viscosus* (Schrad.) Averett which Averett (2009a) recognized as a distinct genus. Hunziker (1991) had included *S. viscosus* in *Leucophysalis and* later (1995) in *Chamaesaracha*. He returned the species to *Leucophysalis* in his *Genera Solanacerum* (2001). Neither *Capsicophysalis* nor *Schraderanthus* seems to be especially close to *Chamaesaracha* and certainly not congeneric.

Capsicophysalis has a distribution similar to that of *Schraderanthus, Brachistus* and *Tzeltalia*, but *C. potosina* extends farther to the north in the Mexican states of San Luis Potosi and Tamaulipas. Morphologically, *Capsicophysalis* is similar to *Schraderanthus* and *Brachistus* which also have orange or red berries, but the flowers are not in fascicles and, at maturity, the fruiting calyx is reflexed under the berry. Table 1 compares *Capsicophysalis* to *Schraderanthus* and *Chamaesaraccha*. Averett (2009a, 2009b) provides further discussion of the history and taxonomy of *Schraderanthus* and its relationship to *Leucophysalis and Brachistus*, including supporting molecular data from Olmstead et al. (2008) and Whitson and Manos (2005).

Hunziker (2001) placed *Brachistus* in Tribe *Solaneae*, subtribe *Witheringinae* while Olmstead et al., (1999, 2008) place *Brachistus* in Tribe *Physaleae*, subtribe *Physalineae*. *Capsicophysalis* has a strongly accrescent fruiting calyx characteristic of the *Physaleae* as described by D'Arcy and Averett (1996). We therefore include *Capsicophysalis* in *Physaleae*, subtribe *Physalineae*, near *Schraderanthus* and *Brachistus*. All three have bright red or orange-red fruit which is relatively uncommon in the *Physalineae*.

Table 1. Comparative characters of *Capsicophysalis, Schraderanthus,* and *Chamaesaracha.*

	Capsicophysalis	Schraderanthus	Chamaesaracha
Habit	Erect, herbaceous, annual	Erect, herbaceous to woody, annual or perennial	Ascending or spreading perennial herbs
Habitat and distribution	Mesic forest, southern Mexico, Guatemala and Honduras	Mesic forest, southern Mexico, Guatemala	Arid regions of southwestern U.S. and northern Mexico
Inflorescence	1–2 flowers from axils	6–8 flowers from axils, in fascicles	1–2 flowers from axils
Corolla	less than 3 cm wide, w/o maculations in the throat	4–5 cm wide, with green broken maculations in the throat	2–4 cm wide, with white tomentose pads in the throat
Fruit	Red, fleshy berry	Red, fleshy berry	Green, dry berry
Fruiting calyx	Accrescent, reflexing under the berry at maturity, red	Accrescent, rotate to slightly reflexed under the berry at maturity, red	Accrescent, appressed to and partially enclosing the berry, green
Seeds	Testa tuburculate with rod-shaped projections	Testa rugose-reticulate, honeycombed	Testa rugose-reticulate, honey-combed

ACKNOWLEDGMENTS

Marshall Crosby provided helpful comments about the nomenclature and we appreciate the assistance of those herbaria which were visited and those from which specimens were borrowed, GH, LL, TEX, QMEX, US, UAT, and VT. We thank Alan Harvey for assistance with the photographs and distribution map and 3 anonymous reviewers for their corrections and helpful comments on the manuscript.

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BOOK REVIEWS

Matt Warnock Turner. 2009. **Remarkable Plants of Texas.** (ISBN 978-0-292-71851-7, hbk.). University of Texas Press, P.O. Box 7819, Austin, Texas 78713-7819, U.S.A. (**Orders:** www.utexas.edu/utpress.com, 1-800-252-3206, 1-800-687-6046 fax, email utpress@uts.cc.utexas.edu). $29.95, 320 pp., color images and photographs, 7 1/4" × 10 1/8".

Remarkable Plants of Texas is a fantastic collection of information on Texas native plants. It includes over 100 magnificent color photographs with informational descriptions of every plant. The 65 plant entries contain one or more similar plants and are separated into plant types: trees, shrubs, herbaceous plants, cacti, grasses, vines, and aquatics. Each plant entry includes helpful information such as common names, scientific family name, botanical description, habitat description, and color photographs of the plant. In addition to the basics, author Matt Turner has included plant uses and location. With regard to uses, Turner notes both historic and current applications. Some of the useful features discussed are wood quality, medicinal value, culinary uses, fiber, building materials, dyes, fragrances, uses as animal fodder, and other economic and social uses.

Remarkable Plants of Texas is a relatively unique book due to the large amount of information on Texas native plants history and uses collected all within one text. As such, Turner has provided a fantastic reference text as well as an entertaining and informative read. It is a wonderful book for considering the way people and plants are connected and interact; not only today, but also historically. Overall, this book is a great collection of facts and plant histories that any plant lover would love to read.—*Lee Luckeydoo Dreese, Volunteer, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

Graham Payne. 2006. **Garden Plants for Mediterranean Climates.** (ISBN-10: 1861268955, pbk.). The Crowood Press Inc., The Stable Block, Crowood Lane, Ramsbury, Marlborough, Wiltshire SN8 2HR, England. (**Orders:** www.crowoodpress.co.uk, by phone 01-672-520320). $35.00, 240 pp., 8 1/2" × 11".

A lavish guide to planning, planting, and maintaining a Mediterranean garden, featuring an A–Z of more than 1,000 plants and 500 color photos. No image of the Mediterranean is complete without flowering climbers, colorful shrubs, or lush gardens. With the help of this book you can enjoy Mediterranean plants in your own garden.

This book includes: an introduction to Mediterranean climate and points to consider when planning a garden; key features of a Mediterranean garden, including climbing plants, palms, pots, and pergolas; sections on both general care and specific plants; advice on watering and soil care; ideas on which plants to use where; an A to Z of more than 1,000 plants; and 500 gorgeous color photos. The core of the book is the A to Z of plants which includes recommended species with photos of some of the cultivars. Each entry includes a general description and growing range, general care notes for specific plants, and cultivation tips. The book includes several special appendixes: meaning of plant names, English common names, and a glossary of terms. A list for further reading concludes the book.

The primary intended audience is for those gardeners who live in a Mediterranean climate, both in and around the Mediterranean basin and elsewhere around the globe. He widens the climate envelope to include anywhere that is frost-fee with a good water supply. The plants he recommends can be enjoyed in both small and large gardens with similar climates or, in cooler regions, in conservatories. Recommended for public libraries and the general reader who is interested in gardening.

Graham Payne trained as a horticulturist and followed a career as a gardener. He became Head Gardener of Downing College, Cambridge, and then Head Gardener of Jesus College, Cambridge, where he oversaw some twenty-seven acres of intensively managed gardens and sports grounds, as well as fifty other properties. He has now retired to southern Europe.—*Gary L. Jennings, Librarian, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

SYNOPSIS OF *GONOLOBUS* S.S. (APOCYNACEAE: ASCLEPIADOIDEAE) IN TRINIDAD AND TOBAGO

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ABSTRACT

A synopsis of *Gonolobus* s.s. (Apocynaceae, Asclepiadoideae, Gonolobinae) in Trinidad and Tobago, including a key, descriptions, and illustrations, is provided to facilitate recognition and conservation of the two accepted species: *Gonolobus rostratus* and *G. tobagensis*. The misapplication of names both in the literature and to South American specimens is discussed.

RESUMEN

Se aporta una sinopsis de *Gonolobus* s.s. (Apocynaceae, Asclepiadoideae, Gonolobinae) en Trinidad y Tobago, que incluye una clave, descripciones, e ilustraciones, para facilitar el reconocimiento y conservación de dos especies aceptadas: *Gonolobus rostratus* y *G. tobagensis*. Se discute la mala aplicación de los nombres en la bibliografía y en los especímenes suramericanos.

About fifty species of subtribe Gonolobinae (Apocynaceae, Asclepiadoideae) occur on the islands comprised by the Greater and Lesser Antilles, the Bahamas, Trinidad and Tobago, and Aruba and the Netherland Antilles. Evidence from the chloroplast (Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006; Krings et al. 2008) and nuclear genomes (Krings et al. 2008) supports the monophyly of the subtribe, as well as of *Gonolobus* s.s. Krings (2008a) recently provided a revision of *Gonolobus* s.s. in the West Indies. However, Trinidad and Tobago were excluded from that treatment due their South American affinity. The objective of this note is to provide a key to and descriptions of the species of *Gonolobus* s.s. from Trinidad and Tobago to facilitate their recognition and conservation.

This treatment is derived from a larger critical study of ca. 250 specimens of the fifty some known species in West Indian Gonolobinae, obtained in part through: (1) loan requests from ninety herbaria—of which sixty-five responded with either loans, digital images, or negative search results (see Acknowledgements), (2) visits to BM, BSC, DUKE, HAC, HAJB, IJ, K, UCWI, UPRRP, US, and P, and (3) forty-eight days of field work by the author in the Bahamas (Long Island), Cuba, Dominica, Jamaica, Puerto Rico, St. Lucia, and St. Vincent. The treatment is also informed by analyses of sequences of portions of the chloroplast (*trnL-F*, *rps16*) and nuclear genomes (*LEAFY*) of selected accessions (see Krings et al. 2008).

TAXONOMIC TREATMENT

Two species of *Gonolobus* s.s. are recognized from Trinidad and Tobago. Descriptions of the species are provided following a key to the species. Corona morphological terminology follows Liede and Kunze (1993) and Kunze (1995): Ca = faucal annulus (corolline corolla); Cd = dorsal anther appendage; Ci = interstaminal gynostegial corona; C(is) = fused staminal and interstaminal gynostegial corona; Cs = staminal gynostegial corona. Species are arranged alphabetically. Following Franz et al. (2008), taxon concept mapping is provided to facilitate databasing. The operator =is used to indicate whether a given taxon concept is equal to a previously published concept. The symbol ≠ is used to indicate the misapplication of a name to a concept.

KEY TO *GONOLOBUS* S.S. IN TRINIDAD AND TOBAGO

1. Calyx lobes ovate, 4.1–8.4 mm × 1.9–5.5 mm, apices obtuse to rounded; corolla lobes glabrous adaxially ________ **1. G. rostratus**
1. Calyx lobes linear-lanceolate, 8.5–13 mm × 1.7–2.6 mm, apices acute to narrowly obtuse; corolla lobes pubescent adaxially ________ **2. G. tobagensis**

1. Gonolobus rostratus (Vahl) Schult. in Roemer & Schultes, Syst. Veg. 6:61. 1820. (**Fig. 1**). *Cynanchum rostratum* Vahl, Symb. Bot. 3:45. 1794. Type: Trinidad: (von Rohr?) Hb. Liebmann (holotype: C [IDC microfiche photo: Vahl herbarium nr. 17: III, 5!]; isotype: BM!).

Gonolobus broadwayae Schltr. in Urban, Symb. Antill. 7(3):340. 1912. Type: Trinidad: *Lopez 2419* (lectotype, designated by Krings 2008b: Z!)

Herbaceous perennial vines. Latex unknown, presumably white. Stems pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter throughout, spreading, or retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.07 mm long; nodes pubescent, gland field apparently absent. Leaf blades ovate to oblong-ovate, 1.9–10.2 cm × 0.9–6.6 cm, apices gradually acuminate with the acumen narrowly obtuse, to 1.2 cm long, bases deeply cordate, margins entire, evenly strigillose on both surfaces, trichomes sharp, eglandular, to 1 mm long, glandular emergences from the surface apparently absent, colleters 2–3, 0.9–1 mm long; petioles 0.9–6.8 cm long, pubescent on all sides, capitate trichomes to 0.16 mm long, sharp, eglandular trichomes antrorsely-ascending or –appressed, ca. 0.7 mm long; stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base (rarely on the stem), ca. 0.3 mm long. Inflorescences racemiform, peduncles 0.4–2.2 cm long, capitate, as well as sharp, eglandular trichomes present, the latter mostly antrorsely-appressed or -ascending, distributed throughout, ca. 0.4 mm long; pedicels 1.2–4 cm long, evenly pubescent from apex to base, capitate-glandular trichomes ca 0.1 mm long, longer, sharp, eglandular trichomes antrorsely-ascending, ca. 0.8 mm long, bracts linear-lanceolate, ca. 5.1–5.5 mm × 0.8–1.1 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, 0.38–0.4 mm long, antrorse. Calyx lobes 5, ovate, 4.1–8.4 mm × 1.9–5.5 mm, apices obtuse to rounded, margins sparsely glabrous or ciliate, abaxial surface sparsely pubescent at the base and glabrous toward the apex, trichomes antrorsely appressed or -ascending, to 0.3 mm long; colleters 1 per sinus. Corolla lobes 5, linear-lanceolate or lanceolate, 12–22 mm × 4.3–6.7 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface glabrous, abaxial surface sparsely pubescent with coarse, sharp, eglandular, antrorsely-appressed or -ascending trichomes, trichomes ca. 0.25 mm long; faucal annulus (corolline corona or Ca) interrupted, a raised bump or indistinct ridge opposite each corolla lobe sinus, pubescent or glabrous; gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, prostrate-undulating, single, secondary nectaries in interstaminal position absent or at least not formed into distinct bumps or mounds; anther guiderails without appendages, laminar dorsal anther appendages (Cd) 1.3–1.5 mm wide, truncate to rounded; style-head ca. 5.4 mm diam, stipe ≤ 0.8 mm long, edentate. Pollinaria: corpuscula ca. 0.23 mm long, pollinia borne horizontally, narrowly ovate, ca. 1.1 mm × 0.4 mm. Follicles apparently known only from a photo taken by P. and Y.S. Comeau, but this was not obtained on loan.

Phenology.—Flowering in March, April, May. Fruiting in March.

Distribution and habitat.—In the Caribbean region, *G. rostratus* is known only from Trinidad, where it has been found on road banks. Its distribution in South America needs to be re-examined (see discussion below).

Etymology.—The specific epithet means "beaked."

Taxon concept mapping.— ≠ *G. rostratus* sensu Schlechter (1899); = *G. broadwayae* sensu Schlechter (1912); = *G. broadwayi* sensu Cheesman (1947).

Notes.—Schlechter (1899) mistakenly listed "*Gonolobus rostratus* Griseb. Flor. ('1861'[1864]) p. 420 (nec R.Br.)" in synonymy with *G. ciliatus* Schltr. The lectotype of the latter, i.e., *Eggers 5561* (P!; designated by Krings 2008b), is referable to "*Matelea*" *denticulata* (Vahl) Fontella & E.A. Schwarz (≡ *Gonolobus denticulatus* (Vahl) W.D. Stevens, if accepting *Gonolobus* sensu lato; holotype: *von Rohr120*, C [IDC microfiche photo: Vahl herbarium nr. 17: III, 1!]; Krings 2008b). For two reasons it seems clear that Grisebach (1864) did in fact mean *G. rostratus* as based on *Cynanchum rostratum* Vahl, rather than "*Matelea*" *denticulata*, when he penned his description. First, he noted the corolla lobes of "his" *G. rostratus* to be lanceolate-linear. Corolla lobes of

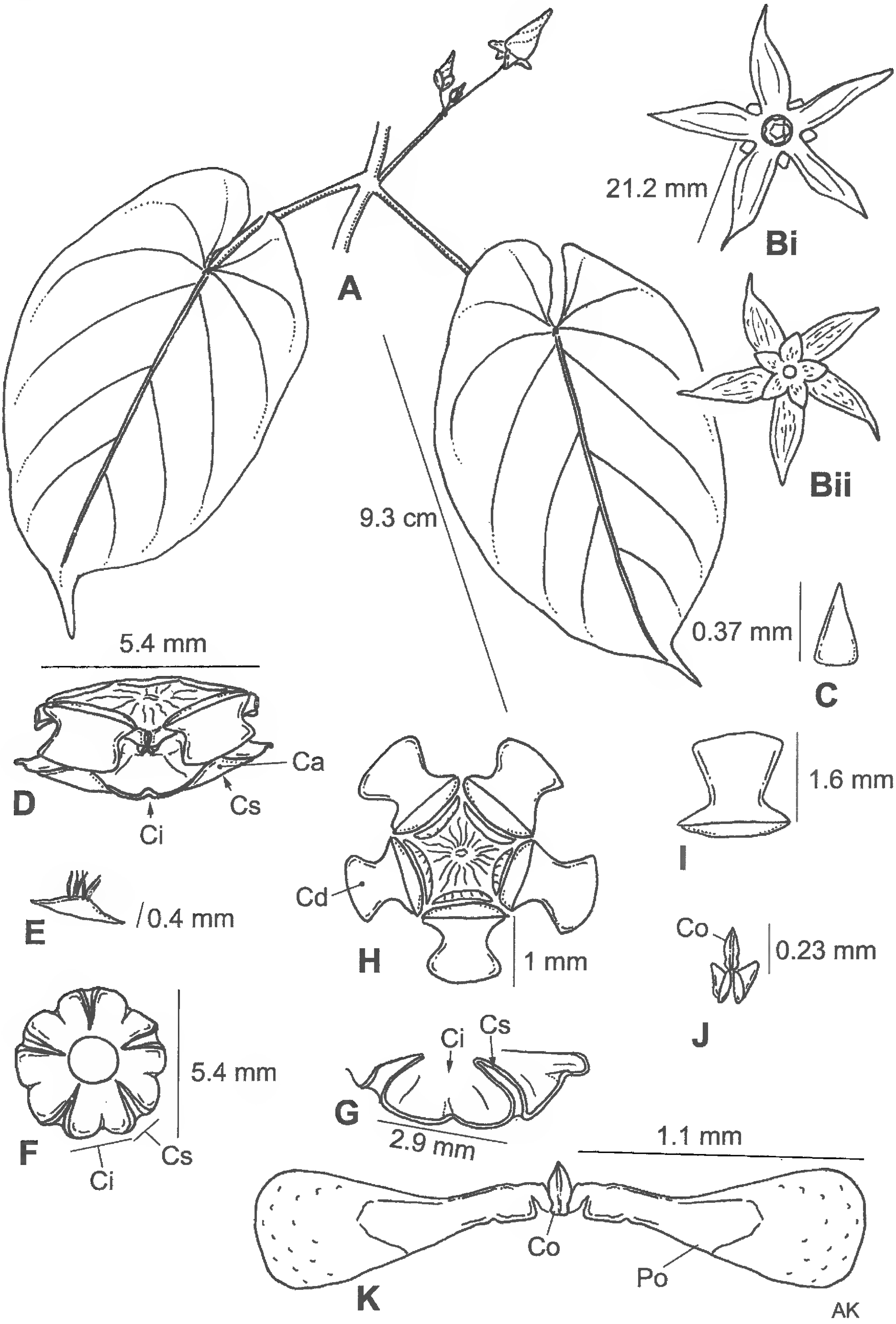

Fig. 1. *Gonolobus rostratus*. **A.** Leaves and inflorescence. **Bi.** Open flower (adaxial view). **Bii.** Open flower (abaxial view). **C.** Calycine colleter. **D.** Faucal annulus of the corolla, gynostegial corona, and style-head. **E.** Detail of faucal annulus. **F.** Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (style-head removed). **G.** Side view of gynostegial corona. **H.** Style-head and laminar dorsal anther appendages (viewed from above). **I.** Laminar dorsal anther appendage. **J.** Corpusculum and subtending anther wings. **K.** Pollinarium. A, C–K based on *Britton & Hazen 1601* (GH). Bi–ii based on *Fendler 637* (E). Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment; Po = pollinium.

"*Matelea*" *denticulata* are broadly elliptic to ovate, whereas those of *G. rostratus* are linear-lanceolate to lanceolate. Second, Grisebach (1864) cited a plate (i.e., t. 7) in Vahl's *Icones illustrationi plantarum Americanarum* (1798), which is so strikingly similar to the holotype of *C. rostratum* at C, as to leave little doubt that it must have been based on it. The ovate calyx lobes of the mature flower are clearly visible in the illustration. A contrasting illustration of *C. denticulatum* (basionym of "*M.*" *denticulata*) is found on plate 8 of the *Icones* (Vahl 1798).

Perhaps following Schlechter (1899), Cheesman (1947) also mistakenly considered "*Gonolobus rostratus* R.Br. sens. Griseb Fl. 420" synonymous with the entity today known as "*Matelea*" *denticulata*, by submerging the former name under a synonym of the latter: *Matelea viridiflora* (G.F.W. Meyer) Woods. Based on Cheesman's description (e.g., "cal[yx] lobes lanceolate," "corolla [...] lobes ovate," "anthers without dorsal appendages"), his concept of *Matelea viridiflora* (G.F.W. Meyer) Woods undoubtedly corresponds to "*M.*" *denticulata* and not *Gonolobus rostratus* sensu Grisebach (1864) and (Vahl) Schult. as discussed above.

The confusion regarding the application of names appears to extend beyond the Caribbean region and affects our understanding of the ranges of *G. rostratus*, *G. tobagensis*, and potentially other species. Fontella & Schwarz (1981) proposed that the following names (and combinations based on them) be added to the synonymy of *G. rostratus*: *Cynanchum rotatum* Vell. (lectotype: Fl. Flum. Icones t. 79!, designated by Fontella & Schwarz 1981), *Gonolobus patens* Decne. (holotype: *Martius s.n.*, M, n.v. [apparently seen by Fontella and Schwarz, but not relocated by M in searches in Fall 2008]), and *G. oxyanthus* Turcz. (holotype: *Funck 2*, G!, P!). As a consequence of this decision, the name *G. rostratus*, has now been applied widely to plants from Tobago to Brazil, Peru, and Argentina (e.g., Fontella & Schwarz 1981; Morellato & Leitão-Filho 1999; Hechem & Ezcurra 2006). Plants from West Africa—considered recent introductions (D. Goyder, pers. comm.)—have been referred to *G. rostratus*, as well. However, based on a preliminary survey of specimen images available to me, including three African collections, it appears that *G. rostratus* may exhibit a much narrower range than presently considered, if not be endemic to Trinidad. The majority[1] of northern South American and African material available to me bearing the name *G. rostratus*, *G. patens*, or *G. oxyanthus* exhibits calyx lobes with acute to acuminate apices, whether linear-lanceolate or ovate, rather than with obtuse to rounded apices as in *G. rostratus* (e.g., Argentina: *Cabrera et al. 32105*, SI; Argentina: *Vanni et al. 83*, K; Argentina: *Venturi 9677*, K, SI; Bolivia: *Wood & Goyder 16744*, K; Ghana: *Merello et al. 1662*, K; Ivory Coast: *Fosberg 40488*, US; Paraguay: *Hassler 227*, SI; Venezuela: *Aristeguieta 6505*, US; Venezuela: *Funck 2*, G, P; Venezuela: *Pittier 11787*, US). In general appearance this material seems much closer to *G. tobagensis*, although I am not convinced that the latter is the correct name nor that a single taxon is represented. Based on the protologue, *Gonolobus patens*, for instance, also exhibits similar linear-lanceolate to lanceolate calyx lobes (Decaisne 1844). The holotype of *G. patens* (Brazil, *Martius s.n.*) resided at M according to Decaisne's (1844) account, but was not recently relocated (F. Schuhwerk, pers. comm.). Fournier (1885) apparently saw this specimen—or at least cited it. He described the calyx lobes of this species as ovate and provided an illustration (t. 94) depicting calyx lobes ovate to lanceolate, but with acute apices, not obtuse as in *G. rostratus* (Fournier 1885). Neither Decaisne (1844) nor Fournier (1885) recognized *G. rostratus* from Brazil. Fontella and Schwarz (1981) were apparently the first to associate *G. patens* and *G. rotatus* with *G. rostratus*. Unfortunately, a complete survey of South American and African entities to which the name *G. rostratus* has been applied is beyond the scope of the present study and limited by the lack of availability of the type of *G. patens*. It appears that either *G. rostratus* displays considerable morphological heterogeneity or that multiple taxa are represented. It is hoped that the key and descriptions provided here will contribute to this much needed survey.

Additional specimens examined: Hab. in Ins. Carib., *Anonymous s.n.* (L). **Trinidad.** Apr [18?]74, *O. Kuntze 881* (E); Morne Cocoa Road, bank, 9 Apr 1920, *N.L. Britton and T.E. Hazen 1601* (GH, K); Gaura Old Rd., 19 May 1937, *Cheesman 13168* (TRIN); 1877–80, *A. Fendler 637* (BM, E); Heights of Aripo Rd., close to small ravine or close to Rhapsey's Estate, Mar 1987, *F. Moreau s.n.* (TRIN); Mar [18?]85, *H. Prestoe s.n.* (K).

[1]One specimen from Peru, *Quipuscoa 378* (K!), has been referred to *G. patens* but departs from the typical form in bearing very long (1cm +) ovate sepals.

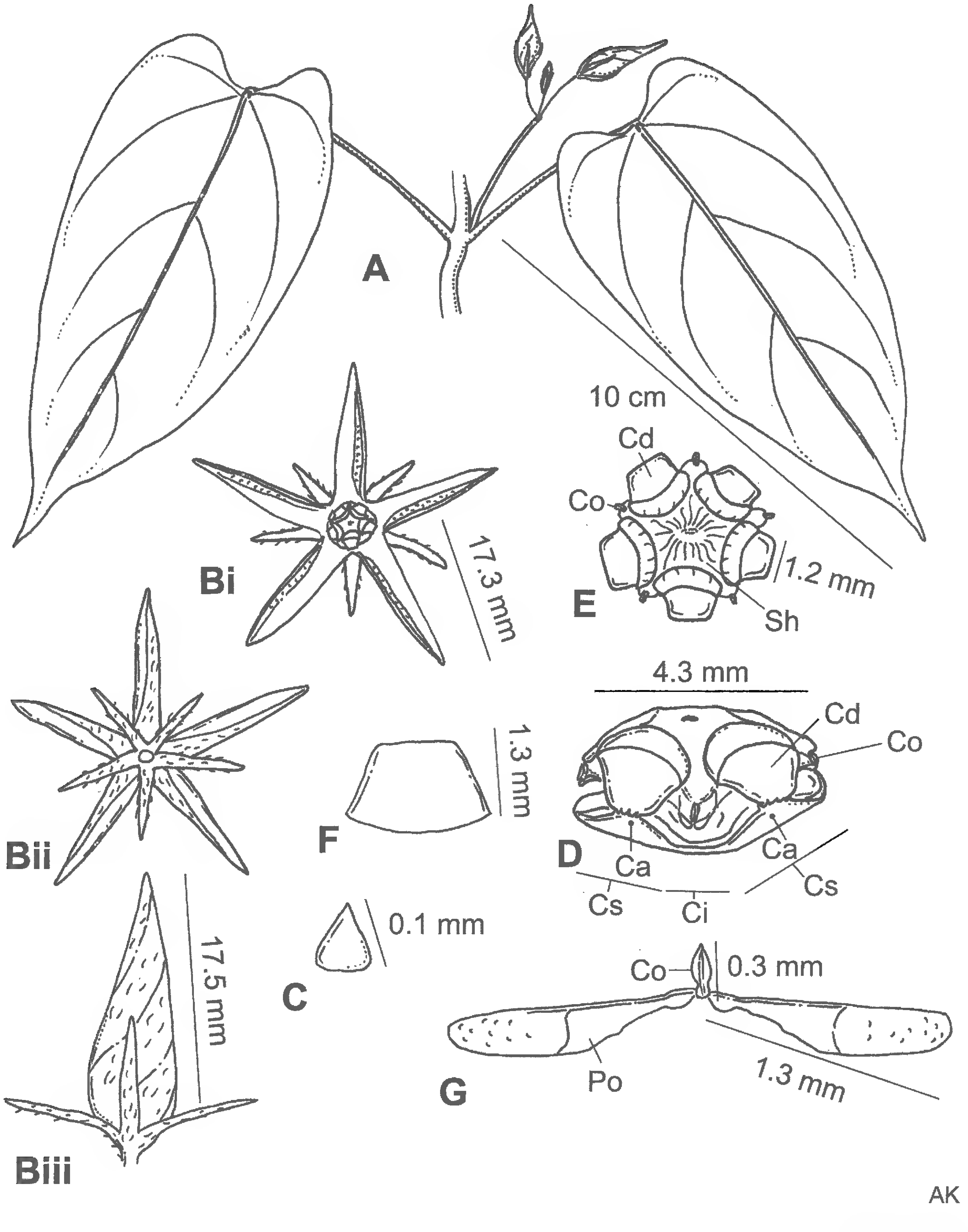

Fig. 2. *Gonolobus tobagensis*. **A.** Leaves and inflorescence. **Bi.** Open flower (adaxial view). **Bii.** Open flower (abaxial view). **Biii.** Flower bud. **C.** Calycine colleter. **D.** Faucal annulus of the corolla, gynostegial corona, and style-head. **E.** Style-head and laminar dorsal anther appendages (top view). **F.** Detail of laminar dorsal anther appendage. **G.** Pollinarium. Based on *Sandwith 1840* (K). Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment; Po = pollinium; Sh = style-head.

2. Gonolobus tobagensis Urb., Repert. Spec. Nov. Regni Veg. 16:37. 1919. (**Fig. 2**). TYPE: TOBAGO: The Widow, a climbing plant, 28 Apr 1913, *W.E. Broadway 4467* (LECTOTYPE, designated by Krings 2008b: BM!).

Herbaceous perennial vines. Latex unknown, presumably white. Stems pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter throughout, spreading, or retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.3 mm long; nodes pubescent, gland field apparently absent. Leaf blades ovate to oblong-ovate, 3–10.8 cm × 1–5.7 cm, apices gradually or abruptly acuminate with the acumen narrowly obtuse, 0.9–1.9 cm long, bases deeply cordate, margins entire, evenly pubescent on both surfaces, trichomes sharp, eglandular, glandular emergences from the surface apparently absent, colleters 2, ca. 0.9 mm long; petioles 1–4.5 cm long, spreading pubescent on all sides, some trichomes capitate, to 0.2 mm long, but mostly sharp, eglandular, to 1.4 mm long; stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base (rarely on the stem). Inflorescences racemiform, peduncles 0.2–4.7 cm long, capitate, as well as sharp, eglandular trichomes present, the latter mostly spreading to somewhat retrorse, distributed throughout, ca. 1.5 mm long; pedicels ca. 3.6 cm long, relatively evenly pubescent from apex to base, capitate-glandular trichomes ca 0.16 mm long, longer, sharp, eglandular trichomes antrorsely-ascending, ca. 1.5 mm long, bracts linear to linear-oblong, 7.6–16 mm × 1.2–2.4 mm, persistent, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.6 mm long, antrorse. Calyx lobes 5, linear-lanceolate, 8.5–13 mm × 1.7–2.6 mm, apices acute to narrowly obtuse, margins sparsely ciliate or glabrous, abaxial surface densely and coarsely pubescent at the base and variously toward the apex, trichomes antrorsely appressed or -ascending, to 0.8 mm long; colleters 1 per sinus. Corolla lobes 5, narrowly lanceolate to elongate triangular, 13.8–18.4 mm × 4.2–5.3 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface papillate-pubescent on the right half, abaxial surface pubescent with coarse, sharp, eglandular, antrorsely-appressed or -ascending trichomes, particularly at the base and variously toward the apex, ca. 0.38 mm long; faucal annulus (corolline corona or Ca) interrupted, a raised bump or indistinct ridge opposite each corolla lobe sinus, pubescent; gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, prostrate-undulating, single, secondary nectaries in interstaminal position unknown (could not be determined from specimens); anther guiderails without appendages, laminar dorsal anther appendages (Cd) ca. 2.9 mm wide, truncate; style-head ca. 4.3 mm diam, stipe ca. 1 mm long, edentate. Pollinaria: corpuscula ca. 0.3 mm long, pollinia borne horizontally, narrowly ovate, ca. 1.3 mm × 0.29 mm. Follicles unknown.

Phenology. Flowering in April, October, and November.

Distribution.—*Gonolobus tobagensis* has been previously considered endemic to Tobago and Trinidad, but was recently cited from Guyana, though not the rest of the Guianan Shield (i.e., not in French Guiana, Surinam, Venezuela: Amazonas, Bolivar, Delta Amacuro; Morillo 2007). In light of the issues presented above, a re-evaluation of the application of this name to South American material is warranted. In Trinidad and Tobago, *G. tobagensis* is known from only four collections (including the type). Its habitat is unclear, but likely mid-elevation rainforests as for other West Indian congenerics.

Etymology.—The specific epithet means "from Tobago."

Taxon concept mapping.— = *G. tobagensis* sensu Cheesman (1947).

Additional specimens examined. **Tobago:** Arima (sp?)-Blanchisseuse Rd. 8th m., 6 Nov 1938, *Cheesman 13357* (TRIN); Mount St. George-Castara Rd (sp?), in forest reserve of Main Ridge, 18 Oct 1937, *N.Y. Sandwith 1840* (K). **Trinidad:** Quare River forests, above the reservoir, 1 Apr 1928, *W.E. Broadway 6876* (MO).

ACKNOWLEDGMENTS

I thank the curators and staff of the following herbaria for searching, or providing access to or loans of their collections: B, BG, BH, BKL, BM, BOLO, BR, BREM, BSC, BUF, C, CGE, COLO, CR, DUKE, E, F, FI, FLAS, FR, FTG, G, GH, GOET, H, HAC, HAJB, HBG, IA, IJ, ISC, JBSD, JE, K, L, LD, LE, LINN (Linnean and Smithean herbaria), M, MICH, MIN, MO, MSC, NCU, NEU, NSW, NY, O, OXF, P, PH, RSA, S, U, UBT, UC,

UCWI, UPRRP, UPS, US, USF, TUR, WILLI, WU, Z. I also thank the following persons for graciously providing images of specimens in their collection cited herein: N. Deginani (SI), L. Gautier (G), D. Goyder (K), A. Lehmann (G), Carolina Loup (P), Marc Pignal (P). The Interlibrary Loan Office of North Carolina State University was instrumental in obtaining titles not in the collection.

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BOOK REVIEWS

Philip V. Wells. 2000. **The Manzanitas of California: also of Mexico and the World.** (ISBN: 0-933994-22-2, hbk.). Originally published by the author, Department of Botany, University of Kansas, Lawrence, Kansas 66045, U.S.A. (**Orders:** check or money orders by mail to Dr. Anke M. Wells, 4638 Bluebird Lane, McLouth, Kansas 66054-3109). $60.00 incl. p&h (plus sales tax for Kansas residents), 151 pp., 8 1/2" × 11".

Published by the author in 2000, this limited edition book is based on more than 40 years of field and herbarium studies of *Arctostaphylos* by the late Philip V. Wells (1928–2004), Professor Emeritus of Ecology and Evolutionary Biology at the University of Kansas in Lawrence, Kansas. His lifelong interest in manzanitas started in the late 1950s while working at the University of California in Santa Barbara and culminated in this 151-page work, the most up-to-date and complete treatise of the genus. The book provides keys, synonyms, descriptions, and distributions for 61 species. Of the 150 illustrations, 146 are published for the first time, including digital scans of nascent inflorescences and endocarp SEMs of all 61 species of manzanitas, a truly ground-breaking work. The attractive hardcover book measures 8.5 × 11 inches and is printed on acid-free paper and bound with red Kivar 7 and gold lettering. Approximately 200 copies are available.—*Craig C. Freeman, Curator (R.L. McGregor Herbarium), Associate Scientist (Kansas Biological Survey), University of Kansas, Lawrence, Kansas 66047, U.S.A.*

David Yetman. 2007. **The Great Cacti: Ethnobotany & Biogeography.** (Arizona-Sonora Desert Museum Studies in Natural History) (ISBN 978-0816524310, hbk.). University of Arizona Press, 355 S. Euclid Ave., Suite 103, Tucson, Arizona 85719, U.S.A. (**Orders:** www.uapress.arizona.edu, orders@uapress.arizona.edu, 1-800-426-3797). $59.95, 297 pp., 8 3/4" × 11 1/4".

The Great Cacti reviews the more than one hundred species of columnar cacti, with detailed discussions of those that have been the most beneficial to humans or are the most spectacular. The book is divided into three principal parts. The first covers the great cacti in general and looks at their uses, ecology, distribution, their origin, evolution, and taxonomy. The second, and largest of the three parts, presents the plants by genera, beginning with capstone species and following with other members of the genus. Some genera are grouped by geographical region, others are not. The third part explores where the hot spots for cacti are. He has not listed sites where he has not personally visited but discusses what he considers to be the most impressive, accessible locations where one can see them in their native lands.

Yetman focuses particularly on northwestern Mexico and the southwestern United States and South America to some degree. He examines the role of each species in human society, describing how cacti have provided food, shelter, medicine, even religiously significant hallucinogens. Yetman shows that the great cacti have facilitated the development of native culture in hostile environments, yielding their products with no tending necessary. He draws upon his experiences and research for earlier books and demonstrates the importance of these plants to the native peoples in these regions. The ethnobotanical uses are listed with each species, generally in a small portion of the first section.

Illustrated by over 300 color photos and color maps, *The Great Cacti* is a marvelous book, one which I enjoyed just paging through. The use of color does not overwhelm the wealth of scientific research he displays throughout his narration. Recommended for public libraries, interested students, and researchers on many levels.

David Yetman is a research social scientist at the Southwest Center of the University of Arizona and host of the television series *The Desert Speaks*, produced by KUAT Television in Tucson and distributed nationally by American Public Television. His books include *The Organ Pipe Cactus* and several books about native peoples and plants. He is co-editor of *Gentry's Rio Mayo Plants: The Tropical Deciduous Forest and Environs of Northwest Mexico*, also published by the University of Arizona Press.—*Gary L. Jennings, Librarian, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

AN OVERVIEW OF THE *DIOSPYROS CAMPECHIANA* COMPLEX (EBENACEAE) AND DESCRIPTION OF THREE NEW SPECIES

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ABSTRACT

The *Diospyros campechiana* complex (Ebenaceae) is described in detail. Six species are recognized for the complex in Mesoamerica, and one species in South America. Expanded descriptions are provided for the three Mesoamerican species, and three new species are described. One new species, **Diospyros camposii,** is confined to a small region on the Pacific Slope of the Sierra Madre del Sur, Oaxaca, Mexico, while two others are known only from Costa Rica, including **Diospyros crotalaria,** which is restricted to the Osa Peninsula, and **Diospyros haberi,** which is widespread in mountainous regions. Members of the complex are remarkable for having fruiting pedicels that tend to hold fast to the calyx, despite being articulated to the receptacle. The fruit itself is weakly attached to the calyx. Photographs, comparison tables, and a key to the species of the complex are provided.

RESUMEN

Se describe en detalle el complejo *Diospyros campechiana* (Ebenaceae). Se reconocen seis especies en Mesoamerica, y una en Sur América. Se aportan descripciones en extenso para las tres especies Mesoamericanas, y se describen tres especies nuevas. Una de las especies nuevas, **Diospyros camposii,** está confinada a una pequeña región de la vertiente pacífica de la Sierra Madre del Sur, Oaxaca, México, mientras que otras dos se conocen sólo de Costa Rica, incluyendo **Diospyros crotalaria,** que está restringida a la Península de Osa, y **Diospyros haberi,** de las regiones montañosas. Los miembros del complejo son notables por tener pedicelos que, a pesar de estar articulados en el receptáculo, tienden a mantenerse firmes hasta el cáliz, mientras que el fruto está adherido débilmente. Las semillas se dispersan probablemente por pájaros. Se aportan fotografías, tablas comparativas, y una clave de especies del complejo.

While examining material during continuing studies of Mesoamerican *Diospyros* (e.g., Provance & Sanders 2005; Provance & Sanders 2006; Provance et al. 2008), building toward production of a comprehensive treatment of the Mexican species, three new taxa belonging to the *Diospyros campechiana* complex were discovered. Because this complex has only been discussed briefly (Provance et al. 2008), here we provide a more detailed account. The addition of three new species brings the number of included species to seven. One of the new species, *D. camposii*, is described from Oaxaca, Mexico, based on collections from a restricted area of the Pacific Slope of the Sierra Madre del Sur, and appears to be a local endemic. Two other species, including *D. crotalaria* and *D. haberi* are described for Costa Rica. *Diospyros crotalaria* appears to be a local endemic restricted to the Osa Peninsula, while *D. haberi* is fairly widespread in the central mountains. Previously described species include *D. campechiana* Lundell, *D. panamense* S. Knapp, *D. hartmanniana* S. Knapp, and *D. juruensis* A.C. Smith. The distribution of the complex extends from Oaxaca and Veracruz, Mexico southward to Panama, and likely enters Columbia, since *D. panamense* has been collected very close to its border. The complex definitely occurs in South America because *D. juruensis* occurs in the Jurua River Basin of the Amazon watershed in western Brazil, where the only known collection was made.

We are unsure about the complete status of this complex in South America because most South American specimens are unavailable for examination. In addition, the protologs of twenty-five recently described species of South American *Diospyros* (Wallnöfer 1999, 2000, 2003, 2005) completely lack photos or other illustrations, and are devoid of comparisons to allied, or even similar-looking taxa. This makes many of them difficult or impossible to place with confidence. Identification keys were also not provided, and no attempt was made to fit them into existing keys (e.g., MacBride 1959; Cavalcante 1963a; White 1981; Sothers & Berry 1998). While not violations of the International Code of Botanical Nomenclature (Greuter

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et al. 1994 2000), the figure omissions are inconsistent with Recommendation 32B, and the omission of comparisons to allied taxa is contrary to Recommendation 32C of the Code. Comparisons among taxa are made in virtually all of the other relevant literature (e.g., Miquel 1856; Hiern 1872; Milbraed 1927; Gleason & Smith 1933; Sandwith 1931, 1949, 1963; MacBride 1959; Cavalcante 1963a, 1963b, 1966, 1977; White 1981; Sothers & Berry 1998; Sothers 2003), and the illustration of types has been standard procedure for most modern taxonomists. Consequently, a more thorough examination of South American specimens may reveal that additional members of the *D. campechiana* complex are present there. However, our examination of the literature and the limited South American *Diospyros* specimens to which we have had access did not reveal any other such species.

The species in this complex are so poorly represented in herbaria that from over fifty herbaria that provided specimens of *Diospyros*, we received only seventy-three specimens (representing fifty collection events) that were referable to species in it. Little or nothing has been recorded concerning bark texture and color, color of the slash, wood characteristics, fruit color, texture and taste, flower odor, and color of the seeds and guard cells in life for most species. Flowers are completely unknown in *D. camposii* and *D. crotalaria*, and male flowers are known from only one or a few collections in the other species. Specimens with female flowers are especially rare: we have seen open female flowers only in *D. campechiana*, and only a single female flower bud in *D. haberi*. Regardless of sex, flowering specimens typically have few open flowers. Fruits seem to be unknown in *D. juruensis*.

METHODS

All of the relevant literature and specimens, including those types we could obtain, were evaluated. Collections were sorted into preliminary groups based on qualitative and quantitative morphological characters, and these groups were considered taxonomic hypotheses warranting continued investigation. Comparisons were then made between specimens assigned to each group and type specimens, specimens determined to be consistent with a species protologue (especially if from near the type locality) and paratypes determined to be consistent with the original description. We also examined specimens in light of floristic and monographic treatments, and the annotations of previous workers. Expanded descriptions have been constructed for previously described species based on the studied herbarium specimens. In this treatment we use 'lanceolate' in the sense of Jackson (1916), being broadest near the lower third of the leaf, not at mid-leaf in the sense of Stearn (2000). Descriptions apply to herbarium material except when indicated, or when obviously referring to fresh material. Map coordinates geo-referenced by the authors are given in brackets. Distribution maps were constructed using The Generic Mapping Tools 4.1.4 (Wessel and Smith 2006) accessed through OMC (Weinelt 2006) and amended using Adobe Photoshop (Ver. CS 8.0, Adobe Systems Incorporated, San Jose, CA). Illustrations are by the first author.

TAXONOMIC TREATMENT

***Diospyros campechiana* complex:** Members of the *Diospyros campechiana* complex are evergreen trees with medium to large, more or less evenly spaced leaves. Petioles and midribs are occasionally transversely fissured, and frequently have a bloom of minute white crystals (scintillae) that are probably derived from cuticular wax, though their origin has not been studied. Stems and leaves are glabrous to sparsely hairy, and members of the complex have been variously referred to as "black strigillose," in reference to *D. campechiana* (Standley & Williams 1967), or "minutely strigillose" in reference to *D. hartmanniana* (White 1978). At low magnification the vestiture appears to be comprised of minute, mostly black, appressed, fusiform hairs. At higher magnification it becomes evident that most hairs are dark red and 2-armed, with a short basiscopic arm, and a longer acroscopic arm. Less often hairs are simple, and in some species there may be a high frequency of similar, but paler, yellowish, or reddish brown hairs. In addition, some taxa are minutely hirtellous or minutely pubescent, with hairs much smaller than those of the aforementioned strigillose vestiture. Stems sometimes have localized patches of atypical hairs (e.g., upright, aspergilliform, etc.) which

we think represent endophytic fungi. In this paper the term "strigillose" refers to the common vestiture of dark red to black, simple and 2-armed hairs, with the addition of modifiers for special cases (e.g., "reddish brown strigillose").

The abaxial lamina surfaces typically have some conspicuously darkened guard cells (Fig. 1), and in all species except *D. campechiana*, the stomatal apparatus is recessed, giving the epidermis a black-puncticulate appearance at 20× magnification. The black dots on the abaxial lamina surface of *D. hartmanniana* that were interpreted by S. Knapp (1997) to be the bases of broken hairs may have been these pigmented guard cells. We suspect that darkening of guard cells is a result of secondary compound degradation in non-functioning cells of older leaves.

Male inflorescences are (1–)2–23(–29)-flowered glomerules, compact cymes, paniculiform cymes, or occasionally fasciculate cymes, in leaf axils of young stems. Their axes are 4-angled, and more densely hairy than leaves and stems, though the hairs are otherwise similar. Female inflorescences are solitary or 2–5(–10)-flowered cymes in leaf axils of young stems, and often more or less 4-angled.

Flowers have 4–5 calyx and corolla lobes, though rarely a calyx or corolla will have only 3 lobes. Corollas are urceolate and white in life, though they turn dark brown upon drying. Male flowers have 10–28 stamens with their filaments fused into 5–14 pairs (comprised of an inner and outer member). Filaments are adnate to the base of the corolla or inserted on the receptacle. Filaments and/or anther connectives are sericeous. The apex of the anther is tapered to rostrate, and consists mostly of minutely muricate connective tissue. The pistillode in male flowers is markedly lobed, with the number of lobes being equal to, or slightly less than, the number of stamen pairs surrounding it. In *D. campechiana* the filaments of adjacent stamen pairs are separated by these lobes, and in *D. panamense* and *D. hartmanniana* the indentations between the lobes resemble impressions of the filaments, suggesting that pressure from filaments against the pistillode during floral development may be responsible for the lobe pattern on the pistillode.

Female flowers in *D. campechiana* possess eight unpaired staminodes, with several short hairs on the abaxial surface of the connective, and lanceolate antherodes with slits. Open female flowers and their internal structures have only been observed in this complex in this one species, though a single mature flower bud has been observed in *D. haberi*. Despite female flowers being largely unknown in the complex, styles often persist on fruits, and their number (1–2) and morphology are useful in species identification.

The female calyx accresces during enlargement of the developing fruit, though not as markedly as in members of the *D. rosei* complex. The fruiting calyx tube is patent ("saucer-shaped" sensu White 1978; Knapp 1997) with a short basal protuberance. The apex of the fruiting pedicel is 4-angled, ± pyramidal in shape, and is jointed to the receptacle within the protuberance at the base of the calyx. Although *Diospyros* is typically described as having fruits with a persistent calyx (e.g., Wallnöfer 2001), members of the *campechiana* complex have a fruit that is weakly attached to the calyx. Despite having a pedicel with an articulated apex (as in other *Diospyros* species), in members of this group the fruit often detaches from the calyx, while the connection of the pedicel apex to the base of the calyx holds firm.

The fruits of members of the complex are small to medium-sized, ovoid-ellipsoid or depressed-globose to subglobose, and reportedly green, yellow, orange, or red when mature. Comparing fruit shape between species is not straightforward, since it is highly influenced by the number of seeds that develop. Fruits are usually asymmetric (e.g., Figs. 4b, 6b) when seeds only develop on one side. The fruits have only a small amount of flesh, which is reddish and vitreous when dry, though possibly viscous and clear in life. There are 1–4 locules separated by complete septa in the taxa in which fruit anatomy was studied. Based on fruit lobes, this also seems to be the case in the remaining taxa. Each locule contains a lone seed which lacks adherent pericarp. The large locules include considerable space around the seeds, and when dry fruits are shaken they produce a rattling sound.

The combination of brightly colored small to medium-sized fruits, that readily separate from the calyx, and contrasting black or very dark inflorescence branches, suggests avian seed dispersal in the complex. We suspect that dispersal in the *campechiana* complex is effected by removal of the fruit from the calyx,

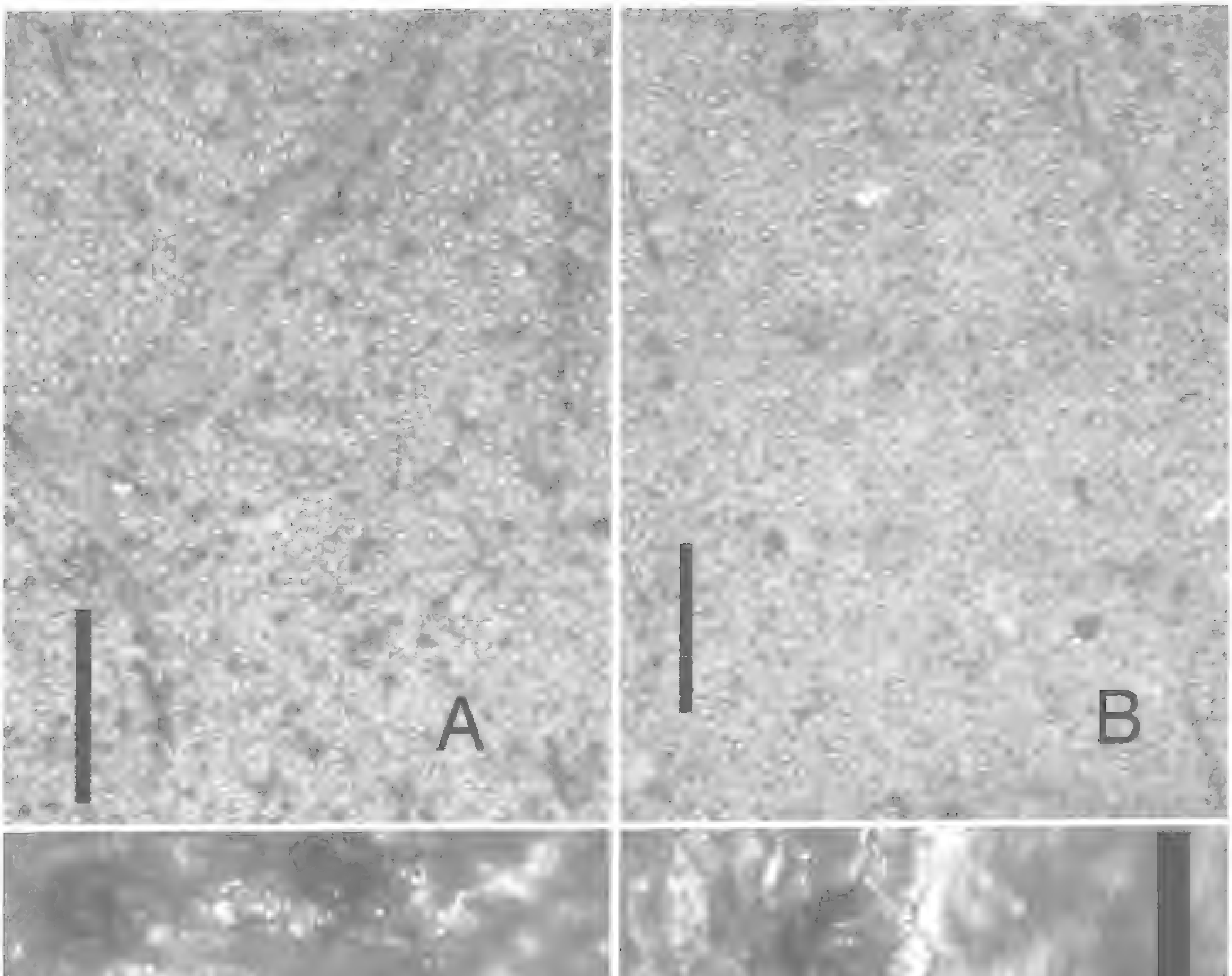

FIG. 1. Epidermis details in species of the *Diospyros campechiana* complex. **A.** Abaxial leaf surface of *D. camposii* (scale = 0.5 mm) from *A. Campos V. & R. Torres C. 825* (MO). **B.** Abaxial leaf surface of *D. crotalaria* (scale = 0.5 mm) from *R. Aguilar 2877* (K). **C.** Pigmented and non-pigmented guard cells on the abaxial leaf surface of *D. hartmanniana* (scale = 0.125 mm) from *G. McPherson & N. Hensold 15310* (B-100152291). **D.** Pigmented and non-pigmented guard cells on the abaxial leaf surface of *D. crotalaria* (scale = 0.25 mm) from *R. Aguilar 2877* (K).

and swallowing of the fruit whole, unlike in other groups (e.g., the *salicifolia* complex), where fruits are torn open and seeds are swallowed incidentally along with adherent pericarp (White 1978; Provance pers. obs.). Alternatively, the combination of detachment of the fruit from the calyx and air space surrounding seeds in mature fruit may suggest a hydrochorous dispersal syndrome (Kubitzki & Ziburski 1994).

Diospyros campechiana Lundell, Contr. Univ. Michigan Herb. 4:23. 1940. (**Fig. 2, 3, 15b**). TYPE: MEXICO. CAMPECHE: Palizada, [18° 15'N, 92° 05'W, 3 m], 25–28 Jul 1939, *E. Matuda 3843* (HOLOTYPE: MICH; ISOTYPES: F, K!).

Trees 6–20 m tall, evergreen; **trunk** up to 45 cm dbh, bark unknown, latex reportedly yellow to orange; **young stems** smooth to shallowly furrowed, brownish, usually dark, viscid, sparsely to moderately strigillose, also densely hirtellous, the hairs minute, light gray to ± colorless, shorter than the appressed hairs; **mature stems** lenticellate, glabrate. **Leaves** alternate, simple, entire; **petioles** 6–17 mm long, minutely hirtellous, sometimes with a few transverse fissures, rounded below, the epidermis longitudinally wrinkled, often scintillant, ± flat above, somewhat canaliculate distally; **lamina** subcoriaceous, oblong-lanceolate to oblong-elliptic, sometimes oblong-oblanceolate, 100–285 mm long, 35–90 mm wide, length to width ratio ca. 2.1–3.5 **:** 1, *base* acute to attenuate, sometimes tapering, usually decurrent on the petiole, *margin* revolute, *apex* acuminate with a rounded tip; **lower lamina surface** dull brown, glabrescent to strigillose, guard cells sometimes conspicuously darkened, but not recessed; **upper lamina surface** dull brown to somewhat glossy, usually papillose. **Venation** eucamptodromous to camptodromous; **midrib** ± rounded below, longitudinally wrinkled, depressed above, sparingly and minutely hirtellous and strigillose near the base of the lamina; **lateral veins** 7–12 per side, prominent below, slightly raised above; **3° veins** slightly raised below, more so above. **Laminar extrafloral nectaries** on the abaxial surface only, common, round to elliptic, 0.3–0.5 mm long, minutely rimmed, drying dark green to black. **Male inflorescences** a single (3–)6–23(–29)-flowered compound cyme in the leaf axil of young stems (sometimes bordering on being a fascicle of 2(–3) cymes), 5–17(–31) mm long, initially paniculiform, but the terminal and often the penultimate units dichasia, axes 4-angled, densely strigillose, also minutely hirtellous, sulcate, subtended by ovate to triangular, concave bracts ± 1 mm long; **peduncles** 1.5–5.5 mm long; **pedicels** 0–1.5 mm long. **Male flowering calyx** subcrateriform (urceolate prior to anthesis), with a short basal protuberance, exterior drying dark brown to black, strigillose, papillate, interior glabrate to locally strigillose, 2–2.4 mm wide, **tube** ± 0.7 mm long, **lobes** 4–5, depressed-orbicular to widely ovate, 0.8–1 mm long, 0.8–1.4 mm wide, sometimes emarginate, often slightly asymmetric, suberect; **male corolla** white in life, drying brown, glabrous except for some minute papillae, **tube** urceolate, 1.2–1.7 mm long, ± 2.3 mm wide, **lobes** (3–)4(–5), 1–1.6 mm long, 1.4–1.9 mm wide, depressed-orbicular to widely ovate, sometimes emarginate, often slightly asymmetric; **stamens** (12–)16(–20?), with Whitefoord and Knapp (1998–onward) reporting 12–16 stamens and Pacheco (1981) reporting 16 stamens, these inserted on the receptacle, fused near the base of their filaments into (6–)8(–10?) pairs, the outer stamen larger, bowing inward at the middle, **anthers** yellow, sometimes with minute red spots, lanceolate, outer anthers 1–1.2 mm long (including the connective), sericeous on the abaxial surface along the connective and sometimes on the adaxial surface, hairs yellow to reddish black, inner anthers similar except smaller, less hairy, and the hairs mostly on the adaxial surface, the apex (connective) tapered, minutely muricate, **filaments** 0.2–0.8 mm long, sericeous near the base of the anther; **pistillode** rotate, markedly 8(–10)-lobed, 0.7–1 mm wide, glabrous, with 2(–1) broadly rostrate apical structures. **Female inflorescences** 1–3 compound cymes in leaf axils on young stems, paniculiform, but the terminal units dichasia, (1–)3–5(–10)-flowered, though no more than three fruit seen on a single inflorescence, 5–8 mm long, axes 4-angled, strigillose, also minutely hirtellous, sulcate, subtended by persistent bracts similar to those of male inflorescences; **flowering peduncles** 0.5–2 mm long; **flowering pedicels** 0.5–2 mm long; **fruiting peduncles** 4–6 mm long; **fruiting pedicels** 2–5 mm long, with a 0.4–0.5 mm long, 4-angled, pyramidal apex, only the distal 0.2–0.3 mm forming a joint within the basal protuberance of the calyx. **Female flowering calyx** campanulate-infundibuliform to crateriform (urceolate prior to anthesis), with a short basal protuberance, exterior drying dark brown to black, moderately strigillose, minutely papillate, ca. 2.5 mm wide, **tube** 1.2–1.5 mm long, **lobes** 4–5, depressed orbicular, (1.1–)1.7–1.9 mm long, 1.5–2.5 mm

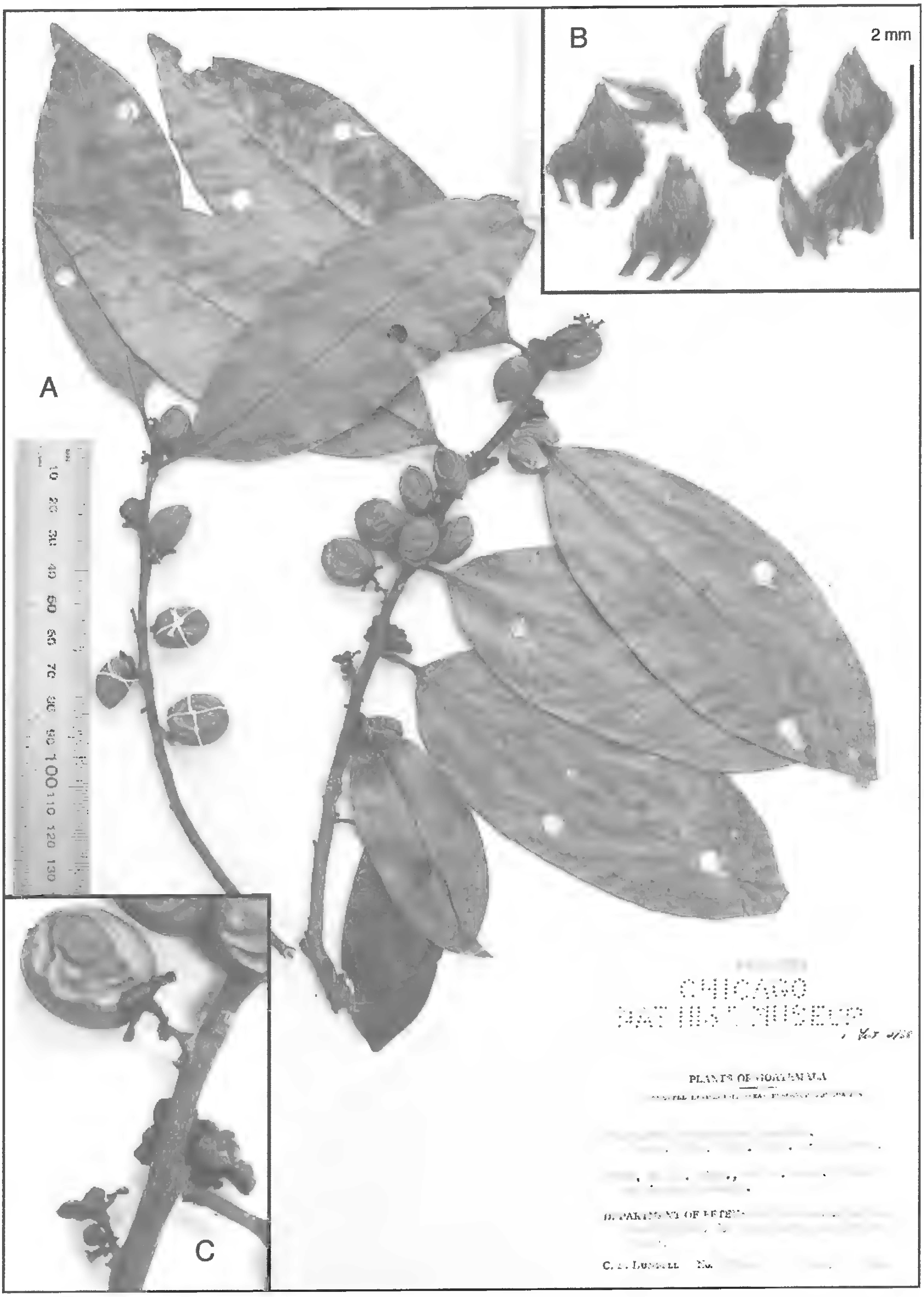

Fig. 2. *Diospyros campechiana*. A. Fruiting stems (*C.L. Lundell 17840*, F). B. Stamens and pistillode (*C.L. Lundell 20739*, MO). C. Inflorescences with persisting calyces. (*C.L. Lundell 17840*, F).

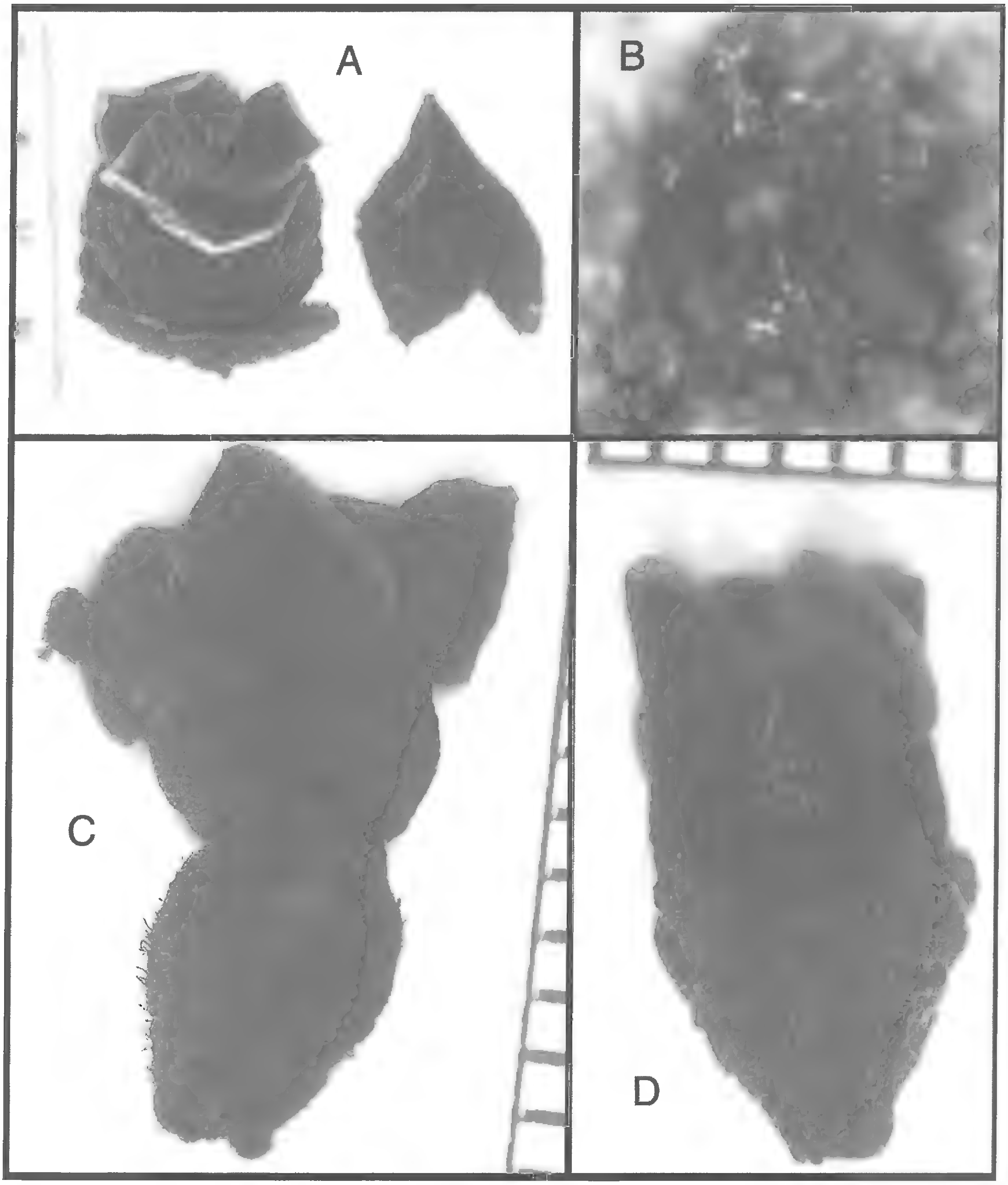

FIG. 3. Diospyros campechiana. A. Male flower (*C.L. Lundell & E. Contreras 20739*, MO). B. Pistillode (*C.L. Lundell & E. Contreras 20739*, MO). C. Female flower (*L. Pacheco & J.I. Calzada 20*, XAL). D. Female flower (*L. Pacheco & J.I. Calzada 20*, XAL).

wide, erect; **female flowering corolla** white in life, drying brown, **tube** 0.9 mm long, 1.3–1.5 mm wide, slightly constricted distally, **throat** 1.2 mm long, semiglobose to urceolate, 2.3–2.5 mm wide, **lobes** 4–5, widely ovate, 1.7–1.9 mm long, ca. 1.6 mm wide, erect (*L. Pacheco & J.I. Calzada 20*) or spreading slightly (*W.E. Harmon & J.A. Fuentes 5790*); **pistil** ± globose, glabrous; **style** 1–2.1 mm long, glabrous, the basal portion 4-angled, divided from the basal 1/3 to 1/2 into two ascending branches (style and stigma [see below] details based on those seen in flowering material and persisting on fruit); **stigmas** minute, undulating irregularly along the abaxial perimeter of the style branches; **staminodes** 8, with several short hairs on the abaxial surface of the connective, antherodes lanceolate, with slits. **Fruiting calyx** not markedly accrescent, relatively thin (not fleshy), drying very dark, exterior glabrate to strigillose, minutely glandular punctate (punctae developing from the minute papillae of flowers), **tube** patent, with a basal protuberance 0.8–2 mm long and 1.5–2 mm wide, the tube 3.5–6 mm wide between opposing sinuses, interior glabrate to moderately strigillose, sometimes minutely glandular punctate, scattered clavate glandular hairs sometimes present, a circular band of short reddish black hairs sometimes present at the base, **lobes** spreading, (2–)2.5–4 mm long, (3–)4–5(–6) mm wide, depressed orbicular, margins repand, sometimes partly revolute, ciliate, adaxial surface glabrate to moderately strigillose. **Fruit** glabrous, (10–)13–17 mm long, 10–17 mm wide, ovoid-ellipsoid, often asymmetric, *locules* 1–4, separated by complete septa; **flesh** sparse to negligible, red and vitreous when dry, unknown in life, though likely viscous and clear; **epidermis** probably smooth in life, usually wrinkled when dry, color progressing from green to yellow to orange with maturity (rarely reported to be red), orange to dark brown when dry; **seeds** 1–4, reddish brown to brown, loosely contained in the fruit, ovoid to ellipsoid, the shape depending on the number of seeds that develop, circular in x.s (when one seed develops), or with 1–2 flat surfaces (when 2–4 seeds develop), 9.5–12 mm long, 5.7–8.4 mm wide, the dorsal surface with a prominent vascular strand, texture rugulose-foveolate, hilum apical on a minute protuberance.

Diospyros campechiana is probably most closely related to *D. camposii*. Separation of these taxa is discussed under the description of the latter. Generally, *D. campechiana* is an easy species to identify. In addition to the geographical separation of this species from other members of the complex, the narrow oblong leaves are distinct, being reminiscent only of *D. crotalaria*. However, the minutely hirtellous vestiture of the stems, petioles, midrib, and inflorescence seems to be diagnostic.

Fruits in fragment folders that have retained their calyx often have the broken tip of the pedicel apex lodged inside the protuberance of the calyx. Thus, in many cases, fruits and calyces that broke away as a unit during the collection process, did not separate from the mother plant at the point of articulation of the pedicel and receptacle/calyx, but rather the pedicel broke near the opening of the cavity in the protuberance at the base of the calyx.

It seems likely that pressure from filaments during floral development creates the lobed pattern on the pistillodes of species in this complex. Because we observed mostly 8-lobed pistillodes in this species, we surmise that the stamen number is usually about 16.

Distribution and ecology.—Diospyros campechiana occurs in lowland tropical forests associated with wetlands and riparian areas of major river systems and their tributaries between sea-level and 270 m elevation in the states of Tabasco, Campeche, Chiapas, and Veracruz, Mexico, and Guatemala (Fig. 5).

Specimens examined. **MEXICO. Campeche. Mpio. Palizada:** 20 km de Palizada hacia el entronque a Escárcega, 18° 07' 19"N, 92° 07' 15"W, [0–4 m], 2 Dec 2000, *P. Sima et al. 2555* (MO). **Chiapas. Mpio. Ocosingo:** a 3 km al S de Frontera Corozal, paralelo a Río Usumacinta, selva alta perennifolia, [near 16° 49'N, 90° 53'W], 120 m, 17 Aug 1984, *E. Martínez S. 7326* (CHAPA). **Tabasco:** "Habitat ad margins fluvii Gonzalez," [18° 15'N, 92° 55'W, 10 m], 8 May 1889, *J.N. Rovirosa 482* (K). **Mpio Jalapa:** 4 km de la desviación carretera Xalapa-Tacotalpa, potrero, [near 17° 50'N, 92° 48'W], 10 m, 22 Nov 1983, *F. Ventura A. 20785* (MO, XAL); Mpio. Comalcalco, San Cayetano, potrero, [18° 22'N, 93° 13'W], 0 m, *F. Ventura A. 20796* (MO, XAL). **Mpio. Jalapa–Tacotalpa:** en el cerco de un potrero, 10 m, 23 Nov 1983, *R. Curiel A. & M.A. Guadarrama O. 108* (CHAPA, XAL). **Mpio. Macuspana:** 8 km de la entrada de Macuspana hacia Escarcega y 1.5 km al N, selva inundable, asociado con *Pachira, Bactris*, [near 17° 41'N, 92° 34'W, 45 m], 25 Aug 1981, *M.A. Magaña A. & S. Zamudio 358* (XAL). **Mpio Nacajuca:** Tucta, a 2 km de Incunac, selva median caducifolia, 2°, suelo cafe super-arcilloso anegado, [18° 12'N, 92° 59'W], 26 m, 6 Oct 1978, *J.I. Calzada 4906* (XAL). **Veracruz. Mpio. Ignacio de la Llave:** [probably the town of Ignacio de la Llave], acahual, [18° 43'N, 95° 58'W], 50 m, 13 Nov 1967, *G. Martínez C. 1555* (USF); 500 m de donde empieza la desviacion Villa Nueva–Zacate Colorado,

en potrero, 18° 43'N, 95° 59'W, 50 m, 29 Apr 1981, *L. Pacheco & J.I. Calzada 20, 21* (XAL). **Mpio. Las Choapas:** Las Choapas, orillas del Rio Playas, cerca de Abasal (one sheet indicates "Rio Playas, arriba de Abasal"), [near 17° 45'N, 93° 57'W], 30 m, 4 Aug 1984, *Miguel Chazaro & Luis Robles 3081* (XAL-2 sheets). **GUATEMALA. Alta Verapaz:** Sebol, along Rio Sebol, in high forest, [15° 48'N, 89° 57', 153 m], Aug 1964, *Elias Contreras 5354* (F, MO); Sebol and vicinity, [15° 48'N, 89° 57', 153 m], Aug 1964, *Elias Contreras 5355* (IJ, F digital image); Chahal, bordering Rio Chiyú, 1km W, in low forest, [near 15° 50'N, 89° 34'N], 29 Oct 1968, *Elias Contreras 8032* (F, MO). **Peten:** La Cumbre, km 142 of Cadenas Road, in low forest on wet land, [16° 05'N, 89° 21'W, 270 m], 24 Sep 1966, *Elias Contreras 6220* (F); Rio Pasion, Altar de Sacrificios, in high forest on bank of river, [16° 30'N, 90° 32'W, ± 380 ft], 8 Feb 1964, *C.L. Lundell 17840* (F, IJ, MO); El Rosario, the FAO-FYDEP Camp at Sayaxche, from thickets along small laguna, [16° 31'N, 90° 10'W], 160 m, 19 Jun 1971, *W.E. Harmon & J.A. Fuentes 5790* (UMO); La Cumbre, caserio "Sapurul", bordering arroyo "Sapurul", in zapotal [and] high forest, [near 16° 05'N, 89° 21'W, 270 m], 7 April 1977, *C.L. Lundell & Elias Contreras 20739* (WIS, MO); La Cumbre, Pusila Road, 5 km N, in acahual, [16° 07'N, 89° 21'W, 250 m], 19 Aug 1976, *C.L. Lundell & Elias Contreras 20224* (MO, UCR); Brecha Chinajá, 12 km from Laguna Petexbatun, high forest, [16° 18'N, 90° 08'W, 540 ft], 20 May 1965, *Elias Contreras 5401* (MO).

Diospyros camposii M.C. Provance & A.C. Sanders, sp. nov. **(Figs. 1a, 4, 15c)**. Type: MEXICO. Oaxaca. Mpio. San Jerónimo Coatlán: 41.5 km al SW de San Jerónimo C.[Coatlán], brecha a Progreso, bosque de pino-encino alterado, suelo amarillo arcilloso, 16° 10'N, 96° 59'W, 1550 m, 29 Nov 1990, *A. Campos V. 3452* (holotype: CHAPA!; isotype: MEXU).

Arbor *D. campechiana* Lundell similis, sed fructu longiore, calyce fructifere crassiore, intervallo grandiore inter sinos oppositos, lobis longioribus et reflexissibus in fructibus, et stylo apicoque fructus pilosibus, caulibus, petiolis, costa inflorescentibusque non hirtellis, lamina breviore et marginis minute porcatis, sed non revolutis, differt.

Trees 8–25 m tall, probably evergreen; **trunk** unknown; **stems** brownish, shallowly furrowed when young, sometimes smooth, sparsely strigillose, becoming lenticellate and scaly in older stems. **Leaves** alternate, simple, entire; **petioles** 8–14 mm long, with a short marginal wing distally, sometimes transversely fissured, sparsely strigillose, epidermis scintillant; rounded below, epidermis longitudinally wrinkled, ± flat above, somewhat canaliculate distally; **lamina** chartaceous to subcoriaceous, widely ovate to elliptic, 55–152 mm long, 33–69 mm wide, length to width ratio ca. 1.5–2.5 **:** 1, *base* acute to shortly-attenuate, sometimes oblique, decurrent on the petiole, *margin* minutely ridged, *apex* acuminate with a rounded tip; **lower lamina surface** dull brown, sparsely strigillose, the hairs densest near the leaf base, many guard cells darkened and often recessed; **upper lamina surface** dull brown, slightly paler than the lower surface, smooth, glabrous. **Venation** camptodromous to eucamptodromous; **midrib** subprominent below, ± rounded, sparsely strigillose, the epidermis longitudinally wrinkled, somewhat raised above with a narrow central canal, glabrous; **lateral veins** (5–)6–9(–11) per side, fine, but prominently raised below, flush or slightly raised above; **3° veins** fine, conspicuously raised below, barely raised above. **Laminar extrafloral nectaries** on abaxial surface only, uncommon, mostly in the proximal half of the lamina, ± round, ca. 0.25 mm wide, green to black. **Male inflorescences** unknown. **Female inflorescences** not seen with flowers, apparently cymes, 1–3 in leaf axils of young stems, each 1–3-flowered, though no more than a single fruit seen on any inflorescence, axes subterete, moderately to densely strigillose, **fruiting peduncle** 0.5–2 mm long; **fruiting pedicel** 1.5–5 mm long, with a 4-angled pyramidal apex jointed to the receptacle within the basal protuberance of the calyx, subtended by 2–3 lanceolate bracts, ca. 2mm long. **Female flowers** unknown, except the **style** at least 2.4 mm long and 0.5 mm wide, hairy, the hairs off-white to reddish, up to 0.7 mm long, ± straight, ± terete, divided into two appressed, ascending branches at least 0.7 mm long (style details based on those persisting on fruit). **Fruiting calyx** thick, but not fleshy, exterior moderately strigillose, the epidermis viscid, **tube** patent, with a basal protuberance 1.3–2 mm long, 6–7.5 mm wide between opposing sinuses, interior with numerous minute, reddish hairs, **lobes** 4–5, reflexed, roundish, the margins weakly revolute, 4–6 mm long, 4–8 mm wide, interior glabrescent, viscid. **Fruit** ovoid-ellipsoid, often asymmetric, (15–)18–24 mm long, (11–)13–15(–17) mm in diameter; hairy near the apex, sometimes with hairs similar to those of the style scattered over the distal third, *locules* unknown, probably 1–4; **flesh** unknown; **epidermis** ± smooth, yellow to orange in life when mature, brownish yellow in herbarium material; **seeds** not observed, loosely contained (audibly so) in the locules of dried specimens.

Two of the paratypes (*A. Campos V. 1017*, MO and *A. Campos V. & R. Torres C. 825*, MO) were originally identified as *D. campechiana*, but annotated by R. Durán "No es *Diospyros campechiana*" in 1995. These specimens were later identified as *D. campechiana* by B. Wallnöfer in 1999. While this species is clearly a

Fig. 4. The holotype of *Diospyros camposii*. A. Fruiting branchlet. B. Fruiting inflorescences.

close relative of *D. campechiana*, that taxon is found primarily in lowland tropical forests associated with wetlands and riparian areas of major river systems between sea-level and 270 m elevation in the states of Tabasco, Campeche, Chiapas, and Veracruz, Mexico, and Guatemala, while *D. camposii* has been found only in Oaxaca in cloud forest between 1200 and 1550 m elevation. There is approximately a 300 km disjunction from the nearest populations of *D. campechiana* in the coastal lowlands of Veracruz to the mountains in Oaxaca where *D. camposii* occurs.

Diospyros camposii can be separated from *D. campechiana* by its shorter, widely ovate to elliptic lamina with a minutely ridged, but not at all revolute, margin. Although sometimes elliptic, the lamina of *Diospyros campechiana* is typically longer and more oblong in outline, and the margin is distinctly revolute. While both species are strigillose, *D. camposii* lacks the additional hirtellous vestiture always present in *D. campechiana*. *Diospyros camposii* also has a larger, thicker, fruiting calyx, with reflexed sepal lobes, in contrast to the thinner calyx with spreading lobes of *D. campechiana*. Finally, the fruits of *D. camposii* are longer and have a hairy apex, with the pubescence extending onto the style. The fruits and style of *D. campechiana* are glabrous.

Distribution and ecology.—This species is currently known only from a small area on the Pacific Slope of the Sierra Madre del Sur (Fig. 5), where it is reported to occur in cloud forest (bosque mesófilo) in association with *Alnus acuminata*, *Arbutus xalapensis*, *Chiranothodendron pentadactylon*, *Clethra mexicana*, *Cornus disciflora*, *Dendropanax arboreus*, *Ficus pertusa*, *Inga eriocarpa*, *Ocotea helicterifolia*, *Oreopanax xalapensis*, *Ormosia oaxacana*, *Parathesis brevipes*, *Picramnia lindeniana*, *Quercus candicans*, *Siparuna andina*, *Ulmus mexicana*, *Viburnum elatum* and *Zinowiewia integerrima* (Campos-Villanueva & Villaseñor 1995). The area has a large number of canyons with permanent streams, and soils consisting of a deep layer of organic matter over red clay (Campos-Villanueva and Villaseñor 1995). The holotype was collected in pine-oak forest.

Etymology.—This species is named in honor of the Mexican botanist Alvaro Campos-Villanueva, who collected the holotype, and participated in all known collections of the species. He is also an author of a flora of the Municipio de San Jerónimo Coatlán in the Sierra Madre del Sur.

Specimens examined. **MEXICO. Oaxaca. Mpio. San Jerónimo Coatlán:** 41 km al SW de San Jerónimo Coatlán, cañada de bosque mesófilo, suelo amarillo arcilloso, 16° 10'N, 96° 58'W, 1250 m, 17 Jan 1988, *A. Campos V. 1017* (MO); 12.3 km al N de Piedra Larga, sobre el camino a Progreso, la desviación se encuentra 9.6 km al NE de Piedra Larga, carr. a Miahuatlán, bosque mesófilo en bosque de pino, en cañada, 16° 09' 00"N, 97° 01' 00"W, 1200 m, 16 Dec 1987, *R. Torres C. & A. Campos 10895* (MO). **Mpio. Piedra Larga:** 12.5 km al NE de Piedra Larga, sobre el camino a El Progreso, bosque mesófilo, suelo negro, 16° 10'N, 97° 01'W, 1300 m, 15 Dec 1987, *A. Campos V. & R. Torres C. 825* (MO).

Diospyros crotalaria M.C. Provance & A.C. Sanders, sp. nov. (**Figs. 1b, 1d, 6, 15a**). Type: COSTA RICA. Puntarenas. Cantón de Osa: R.F. Golfo Dulce, Península de Osa, Rancho Quemado, Sector Oeste, 08°, 41' 10"N, 83° 35' 10"W, 400 m, 9 Sep 1992, *J. Marín 512* (holotype: MO-5316690!; isotypes: CR, K!).

Arbor *D. harmanniana* S. Knapp similis, sed lamina oblonga usque oblongo-obovata, fructu glabrato, stylibus glabratis, gracilioribus, erectibusque et divisis prope usque basum, calycis fructiferis gracilibus, lobis reflexis differt.

Trees 10–20 m tall, probably evergreen; **trunk** recorded up to 15 cm dbh, bark reportedly thick; **young stems** reddish brown, somewhat compressed, shallowly channeled, or with some minor furrows, glabrescent to sparsely strigillose, the hairs pale yellow to dark red or nearly black; **mature stems** terete, rugose, densely lenticellate. **Leaves** alternate, simple, entire; **petioles** 4–9(–10) mm long, subterete, epidermis often scintillant, atropurpureous, rugulose, the wrinkles often transverse, sometimes developing into fissures; glabrous to sparsely strigillose, the hairs slightly flexuose, ascending, and pale yellow, or straight, appressed, and dark red to nearly black; shallowly V-grooved above, the groove sometimes with an additional narrow channel down its center, glabrous below, sometimes with a few small longitudinally oriented lenticels; **lamina** subcoriaceous, oblong to oblong-obovate, sometimes narrowly ovate, 74–150 mm long, 26–49 mm wide, length to width ratio ca. 2.5–3 : 1, *base* acute to subacute, *margin* flat, *apex* acuminate with a rounded tip; **lower lamina surface** reddish brown, slightly darker than above, dull, glabrescent or with scattered minute, 0.2–0.5 mm long, straight, appressed, dark red to nearly black, sometimes pale yellow hairs, epidermis sometimes with aggregates of opaque light-colored excrescences, guard cells often very

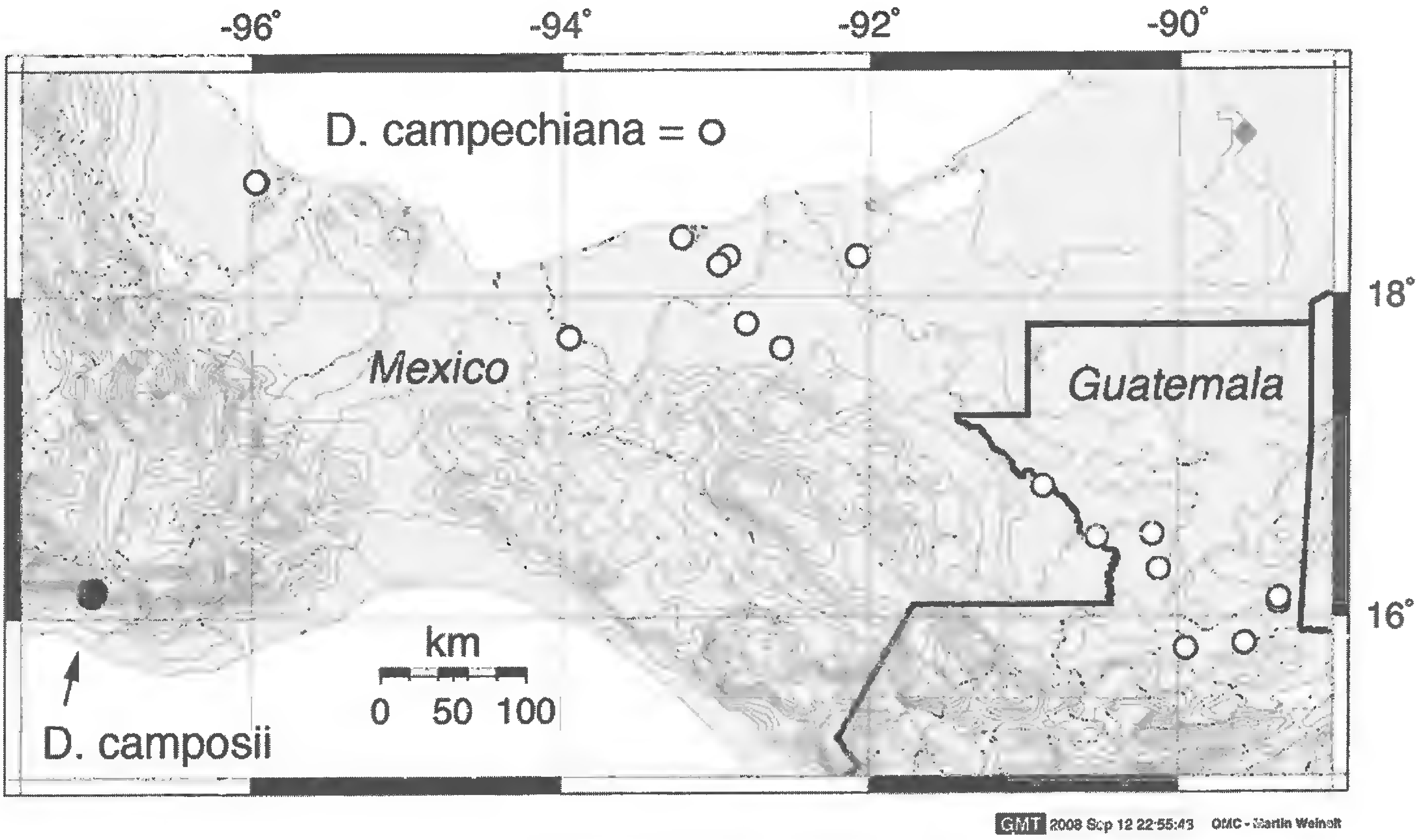

Fig. 5. Distribution of *Diospyros camposii* and *D. campechiana* in Mexico and Guatemala.

dark and recessed, **upper lamina surface** grayish green, not glossy, though slightly more shiny than below, glabrous, epidermis densely papillose, the papillae angular. **Venation** eucamptodromous; **midrib** narrow but prominently raised below, rounded, longitudinally wrinkled, glabrate to sparsely strigillose; shallowly V-grooved above, glabrous; **lateral veins** 6–9(–10) per side, fine, raised below, forming inconspicuous loops with superadjacent laterals, flush or slightly depressed above, papillae absent; **3° veins** fine, inconspicuously raised below, imperceptible above, or barely so, and then depressed. **Laminar extrafloral nectaries** on the abaxial surface only, relatively common, round to elliptic, 0.2–0.5 mm wide, black. **Male inflorescences** unknown. **Female inflorescences** cymes, 1 per leaf axil on young stems, 1–2-flowered, producing 1–2 fruit, axes ± terete, densely strigillose, the hairs flexuose, pale yellow to dark reddish brown, subtended by 2–3 opposite pairs of strigillose, persistent, deltoid bracts; **fruiting peduncle** 0.5–1.5 mm long; **fruiting pedicel** 1–2 mm long, with a 1 mm long 4-angled apex that forms a joint within the basal protuberance of the calyx. **Female flowers** unknown, except **styles** (2) erect, divided ± to the base, 4-angled, at least 0.9 mm long, 0.2 mm wide, essentially glabrous, though a long solitary hair was seen in the style branch fork on two of the known fruit (style details based on remnants from fruit). **Fruiting calyx** relatively thin (not fleshy), reportedly green in life, drying very dark, exterior strigillose, the hairs pale yellow to dark red, epidermis viscid, **tube** patent, with a ca. 1.5 mm long basal protuberance, 5–6 mm wide between opposing sinuses, interior sometimes with numerous minute, reddish hairs, **lobes** 4–5, usually reflexed, ovate, 2.4–3 mm long, 3–4 mm wide, the margins flat to weakly revolute, with a few cilia near the sinuses, moderately pubescent inside, the hairs minute, appressed, pale yellow to dark red. **Fruit** glabrous, 13–19 mm long, 15–20 mm wide, depressed globose to subglobose, often appearing 2–4 lobed (when dry) due to conformation of the fruit wall to the shape of the (1–4) locules with developing ovules; **flesh** exiguous; **epidermis** smooth, yellow in life when nearly mature, drying orangish-brown, red when mature, drying dark reddish brown; **seeds** 1–4, brown, loosely contained in the fruit, ± ellipsoid, 9–11.5 mm long, with 1 or 2 flat surfaces, ca. 6 mm wide, dorsal surface broadly convex, with a prominent vascular strand, texture rugulose-foveolate.

Specimens examined. **COSTA RICA. Puntarenas. Cantónde Osa:** R.F. Golfo Dulce, Península de Osa, Cerro Chocuaco, camino el

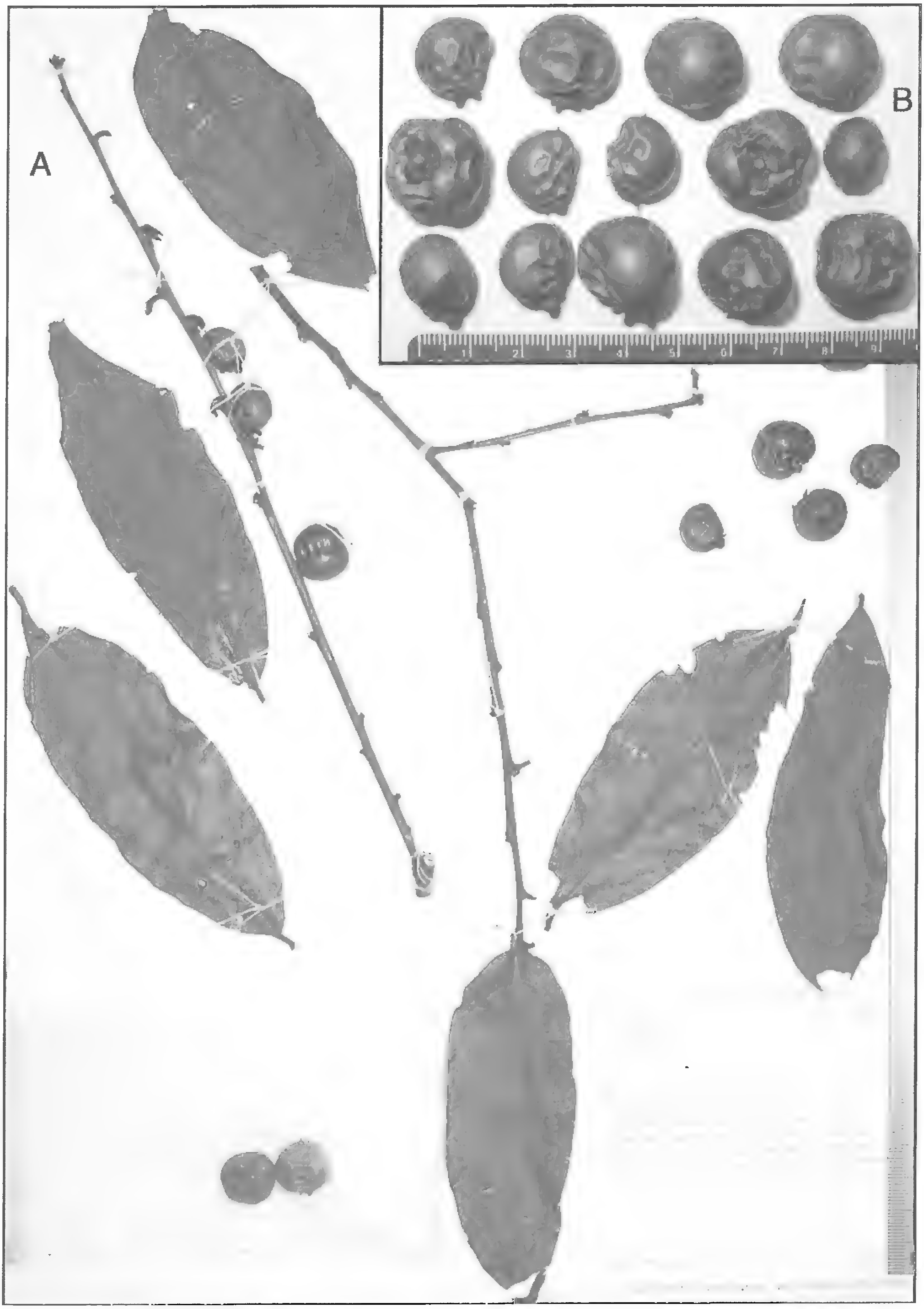

Fig. 6. The holotype of *Diospyros crotalaria*. A. Fruiting branchlet with persisting calyces. B. Fruits.

faro, 08° 43' 20"N, 83° 32' 20"W, 400 m, 28 Dec 1993, *R. Aguilar 2877* (CR, K!, MO!). **Cantón de Golfito Jiménez:** Dos Brazos de Río Tigre, Cerro Müeller (falso Müeller) hasta Cerro Rincón, siguiendo el sendero entre las quebraditas (following the path between the small creeks), 08° 30' 35"N, 83° 28' 15"W, 782 m, 25 Nov 1990, *G. Herrera 4647* (CR, K!, MO!).

The specimens of *D. crotalaria* we examined had not previously been determined to species. *Diospyros crotalaria* is similar to *D. hartmanniana*, but can be separated (Table 1) by its oblong lamina, glabrous fruits, and more slender, glabrous, erect styles, which are divided nearly to the base. Furthermore, *D. crotalaria* has a thinner calyx, and smaller, reflexed calyx lobes.

Distribution and ecology.—Apparently endemic to hills and canyons with wet tropical evergreen forest between 400 and 800 m elevation on the Osa Peninsula on the coast of southwestern Costa Rica (Fig. 14). Reports of *D. hartmanniana* from the Osa Peninsula (e.g., Zamora et al. 2004) may have been in reference to this species. The closest population of *D. hartmanniana* to the Osa Peninsula, that we know of, is about 75 km southeast in Panama.

Etymology.—This species is named for the rattling noise of the seeds in the locules of fruit on herbarium specimens.

Diospyros haberi M.C. Provance & A.C. Sanders, sp. nov. (**Figs. 7, 15d**). Type: COSTA RICA. Alajuela. Cantón de Upala: P. N. Rincón de la Vieja, Cordillera de Guanacaste, sendero La Siembra, c. a 7 km de la casa de Administración, 10° 47' 50"N, 85° 18' 19"W, 1500 m, 6 Jul 1991, *G. Rivera 1422* (holotype: MO!; isotypes: K!).

Arbor *D. hartmanniana* S. Knapp similis, sed lobis calycorum adaxialles prope glabratis, 1.5–2 mm longis, apico laminae rotundo, superficio laminae superioris olivaceo, splendiore clarioreque quam superficio inferioris olivaceo-griseo, uno (raro duobus) style glabrato differt.

Trees 8–28 m tall, apparently evergreen; **trunk** up to 60 cm dbh, the bark reportedly black with white patches; **young stems** 4–5 angled, somewhat compressed and channeled, sulcate, shiny, minutely black gland-dotted, sparsely strigillose; **mature stems** terete, glabrate, the epidermis light to dark green, smooth to half-netted, eventually lenticellate. **Leaves** alternate, simple, entire; **petioles** 3.5–9 mm long, ± terete, epidermis light green to castaneous or atropurpureous, shiny, sometimes transversely fissured, rugulose below, glabrous to sparsely strigillose, rounded above, rugulose and sparsely strigillose, channeled, often deeply, glabrous within or with scattered black hairs; **lamina** subcoriaceous, elliptic, 30–96 mm long, 17–40 mm wide, length to width ratio ca. 1.8–2.7 : 1, *base* acute to attenuate, *margin* flat, though thickened, *apex* acute to obtuse, rarely slightly acuminate; **lower lamina surface** greenish to grayish brown, glabrate to sparsely strigillose, guard cells often dark, the stomatal apparatus often recessed; **upper lamina surface** greenish brown, shinier and slightly lighter than the lower surface, glabrate, epidermis markedly papillose, the papillae angular. **Venation** brochidodromous to eucamptodromous; **midrib** narrow below, subprominent, glabrate to sparsely strigillose, epidermis often darkened, longitudinally wrinkled, shallowly V-grooved above, glabrous or with some scattered dark appressed hairs; **lateral veins** 6–9 per side, fine, raised below, barely raised above; **3° veins** slightly raised below, inconspicuous above. **Laminar extrafloral nectaries** on the abaxial surface only, usually near the midrib and towards the base, round to elliptic, 0.1–0.3 mm wide, dark green to dark brown. **Male inflorescences** solitary compact cymes in leaf axils of young stems, (1–)2–3-flowered, 6 mm long, axes 4-angled, strigillose, subtended by 1–2 pairs of deltate, 0.7 mm long, 0.6 mm wide bracts; **peduncles** 0.3 mm long; **pedicels** 0.3–0.8 mm long. **Male flowering calyx** crateriform to subrotate, exterior drying dark greenish brown, 3 mm wide, **tube** 1.5 mm long, exterior sparsely black strigillose, interior unknown, **lobes** 4, widely ovate, 0.5 mm long, 1–1.3 mm wide, erect, exterior glabrate to sparsely black strigillose, margins densely ciliate, interior glabrous; **male corolla** white in life, drying dark brown, glabrous, **tube** urceolate, 2 mm long, 2.6 mm wide, **lobes** 4, quadrate, 1.4 mm long, ca. 1.4 mm wide; only three flowers were seen, none were dissected, thus stamen morphology is unknown, except that anthers have a slender, tapering connective. **Female inflorescences** solitary, subsessile flowers in leaf axils of young stems, or rarely 2-flowered compact cymes, but no more than a single fruit seen in an inflorescence; axes 4-angled, sparsely strigillose, with 1–2 pairs of persistent, ovate bracts, 0.8 mm long, 1 mm wide; **fruiting peduncles** 0–0.5 mm long; **fruiting pedicels** ca. 0.5 mm long, with a 0.3 mm long

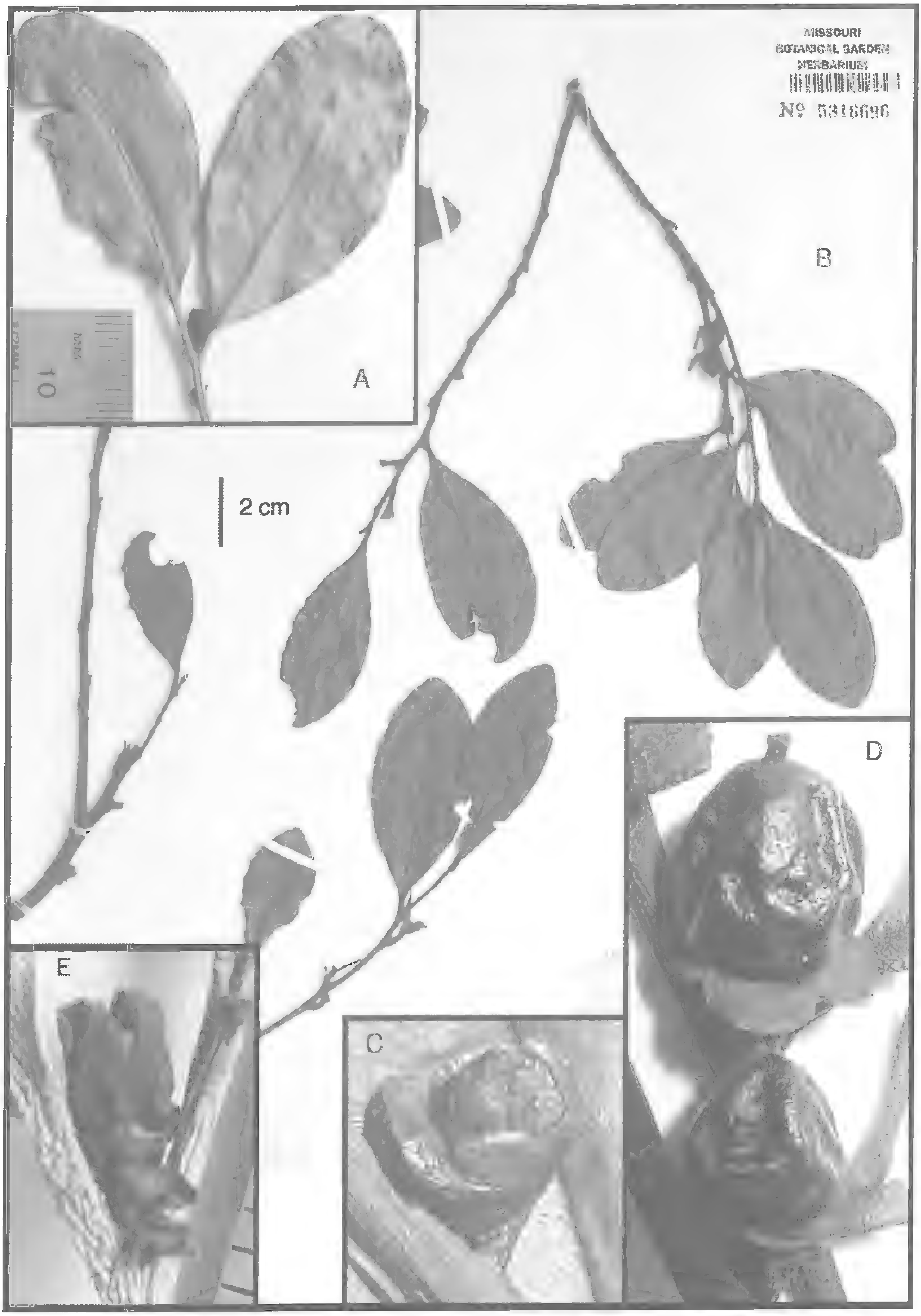

FIG. 7. *Diospyros haberi*. A. Leaves and male flower (*W. Haber & S. Daniel 9895*, MO). B. Branchlets with immature fruits (from the holotype). C. Female flower bud (*G. Rivera 1422*, K). D. Detail of immature fruits (from the holotype). E. Male inflorescence (*W. Haber & S. Daniel 9895*, MO).

Table 1. Morphological comparison of species of the *Diospyros campechiana* complex in Costa Rica and Panama.

	D. panamense	D. hartmanniana	D. crotalaria	D. haberi
Fruiting calyx	thick	thick	thin	thick
Fruiting calyx tube width (distance between opposing sinuses)	7–10 mm	5–6 mm	5–6 mm	5.1–6.6 mm
Fruiting calyx lobe length	2.7–5 mm	2.7–3.8 mm	2.4–3 mm	1.5–2 mm
Fruiting calyx lobe width	4.5–9 mm	(4–)4.4–5.5 mm	3–4 mm	3.8–5.3 mm
Fruiting calyx lobes	spreading to slightly reflexed	± spreading	reflexed	± spreading
Fruit length	up to 33 mm	(14–)17–20 mm	13–19 mm	14–18 mm
Fruit vestiture	glabrous when mature, hairy at apex and base when immature	usually hairy, especially at the base and apex	glabrous	glabrous when mature, hairy at apex immature
Style	1, hairy, minutely deltoid-bifid	1, hairy, divided nearly to the base, spreading in the form of a 'V'	2, ± glabrous, divided to the base, parallel and erect	1(–2), glabrous, shortly deltoid-bifid, often cleft on one side
Stem, petiole and midrib	minutely curved-acicular pubescent	not curved-acicular pubescent	not curved-acicular pubescent	not curved-acicular pubescent
Lamina shape	oblong-elliptic to elliptic, apex acuminate	elliptic, apex acuminate	oblong to oblong-obovate, sometimes narrowly ovate, apex acuminate	elliptic, apex rounded
Lamina size	(96–)127–240 mm long, 45–107 mm wide	(50–)64–163 mm long, 25–70 mm wide	74–150 mm long, 26–49 mm wide	30–96 mm long 17–40 mm wide

4-angled pyramidal apex forming a joint within the basal protuberance of the calyx. **Female flowers** known from a single flower bud and style remnants on immature fruit. **Female flowering calyx** subcampanulate prior to anthesis, sparsely strigillose, 6.3 mm wide, **tube** 2.5 mm long, **lobes** (3–)4, thick (ca. 0.8 mm at 1/4 length), ± evenly tapered to the apex, depressed-orbicular, 1.2–1.8 mm long, 3.9–4.1 mm wide, sometimes emarginate, asymmetric (hooking left viewed abaxially), ciliate on the left margin; **female flowering corolla** drying dark brown, **tube** ca. 2.2 mm long, with some scattered dark two-armed hairs, **lobes** 4, ca. 1.3 mm long, shape and width indiscernible, with some indistinct papillae; **pistil** unknown; **styles** 1(–2), 0.8–1.2 mm long, 0.7–1 mm wide, angular, bifid, the branches short, 0.2–0.3 mm long, deltoid, style often grooved on one side, rarely notched apically or grooved on both sides, glabrous, though strigillose near the base on the apex of the fruit (style and stigma [see below] details based on those persisting on fruit); **stigmas** depressed orbicular, 0.3 mm long, 0.7 mm wide; **staminodes** unknown. **Fruiting calyx** barely accrescent, thick, probably fleshy and green in life, drying brown to black, exterior sparsely strigillose, **tube** patent, with a basal protuberance 1.2–1.5 mm long, 5.1–6.6 mm wide between opposing sinuses, interior glabrous, or with some scattered reddish hairs, **lobes** ± spreading, depressed orbicular, 1.5–2 mm long, 3.8–5.3 mm wide, margins flat to slightly reflexed, ciliate, glabrous inside. **Fruit** 14–18 mm long, 10–20 mm wide, depressed globose to subglobose, often appearing 2–4 lobed when dry due to conformation of the fruit wall to the (1–4) locules with developing ovules, glabrous except for some dark hairs at the apex in immature fruit; **flesh** sparse, reddish, translucent and vitreous when dry; **epidermis** green in life when immature, becoming orange to red when mature, delicate, golden brown to dark reddish brown and loosely wrinkled when dry; **seeds** 1–4 (based on fruit lobes), reddish brown, loosely contained in the fruit, probably

wedge-shaped, 14–18 mm long (width indeterminable, and shape uncertain, as the only seed observed had been sectioned longitudinally), surface texture rugulose in a maze-like pattern.

Distribution and ecology.–This species is associated with moist and windswept forests between 1100 and 1700 m elevation on the Pacific slopes of the Cordilleras de Guanacaste, Tilarán, and Talamanca, in Costa Rica (Fig. 14). Populations occur near, but as far as known do not overlap, populations of *D. hartmanniana* in the former two mountain ranges. All of the specimens examined had been recently identified as *D. hartmanniana*, to which it is doubtless closely related. The most obvious differences between the species (Table 1.) involve leaf apex shape, and style number and morphology. In addition to these characters, the interior of the sepal lobes in male and female flowers of *D. haberi* are glabrous, while in *D. hartmanniana* they are densely dark strigillose. The color and brilliance of the lamina is also different in these species. In *D. haberi* the greenish brown upper surface of the lamina is shinier and slightly lighter than the greenish to grayish brown lower surface. Brilliance is reversed in *D. hartmanniana*, where the grayish brown upper surface is duller than the reddish brown lower surface.

Etymology.—This species is named in honor of William A. Haber, a biologist who has contributed greatly to our knowledge of the biota of Costa Rica and who has documented the presence of this new species at Monteverde.

Specimens examined. **COSTA RICA. Guanacaste. Cantón de Tilarán:** Cañitas, Río Cañas, Lado Pacifico, 10° 20'N, 84° 51'W, 1200 m, 25 Aug 1989, *E. Bello 1124* (MO). **Puntarenas. Cantón de Buenos Aires Olán:** siguiendo filas en cuenca superior de Río Cabagra, 9° 17' 40"N, 83° 11' 50"W, 1700 m, 24 Sep 1989, *G. Herrera 3542* (MO). **Cantón de Osa:** San Luis, Monteverde, Buen Amigo, 10° 16' 00"N, 84° 49' 00"W, 1100 m, 10 Nov 1993, *Z. Fuentes & E. Fuentes 565* (MO). **Cantón de Puntarenas:** Monteverde, Bajo Tigre Reserve, 10° 18'N, 84° 48'W, 1200–1300 m, 3 Apr 1991, *W. Haber & W. Zuchowski 10600* (MO); Monteverde, above Quebrada Máquina, along Fonseca, Hotel de Montaña and Savage Farms, 10° 18'N, 84° 48'W, 1100–1300 m, 3 Jun 1990, *W. Haber & S. Daniel 9895* (MO).

Diospyros hartmanniana S. Knapp, Novon 7:256. 1997. (**Figs. 8, 9, 15e**). Type: PANAMA. Chiriquí: near Coast Rican border, ca. 13 road-km from Río Sereno, Finca Hartmann, 1550–1750 m, 08° 50'N, 82° 45'W, 23 Oct 1992, *G. McPherson & P.M. Richardson 15959* (holotype: BM; isotypes: MO, PMA).

Trees 7–20 m tall, rarely a 1.5 m tall shrub, apparently evergreen; **trunk** up to 72 cm dbh, bark smooth and black, wood oxidizing bright yellow; **young stems** angular, often compressed, sulcate to channeled, shiny, often minutely black gland-dotted, glabrous to sparsely strigillose; **mature stems** dark, terete, smooth, glabrate to sparsely hairy, later half-netted, scaly and lenticellate. **Leaves** alternate, simple, entire; **petioles** 4–10 mm long, subterete, epidermis castaneous to atropurpureous, sometimes transversely fissured, sometimes scintillant, longitudinally wrinkled to colliculate below, shiny, glabrous to strigillose; glabrous above, markedly channeled; **lamina** subcoriaceous, elliptic, (50–)64–163 mm long, 25–70 mm wide, length to width ratio ca. 2–3 **:** 1, *base* acute to attenuate, *margin* flat, though slightly thickened, *apex* acute to subacute, rarely obtuse, acuminate, the tip rounded; **lower lamina surface** reddish brown, glabrate to sparsely strigillose, aggregates of opaque off-white excrescences sometimes present, guard cells often dark and the stomatal apparatus often recessed; **upper lamina surface** grayish brown, duller than the lower surface, glabrous, epidermis conspicuously papillose, the papillae angular. **Venation** brochidodromous to eucamptodromous; **midrib** narrow below, though prominently raised, rounded, longitudinally wrinkled, glabrous to strigillose, the hairs pale or dark; V-grooved above, glabrate; **lateral veins** 6–11 per side, fine, raised below, slightly raised to barely depressed above, lacking papillae; **3° veins** slightly raised below, indiscernible above. **Laminar extrafloral nectaries** on the abaxial surface only, common near the midrib and the base of the lamina, 0.1–0.5 mm wide, castaneous. **Male inflorescences** solitary compact cymes in the leaf axils of young stems, or several near the base of young stems, (1–)3–7-flowered, 7–11 mm long, axes 4-angled, densely reddish brown to black strigillose, subtended by several lanceolate to widely ovate, 1–2 mm long, ca. 1 mm wide bracts; **peduncles** 0.5–1.5 mm long; **pedicels** 0.5–1.5 mm long. **Male flowers** known only from buds. **Male flowering calyx** subrotate, with a basal protuberance ca. 1 mm long, exterior drying dark greenish brown, moderately strigillose, interior densely strigillose, 3.5–4.1 mm in widest dimension, **tube** 1–1.2 mm long, **lobes** 4–5, ovate, 0.9–1.2 mm long, 1.3–1.6 mm wide, suberect to spreading, margins ciliate; **male corolla** white to cream in life, drying dark brown, thick, glabrous, papillate, **tube** urceolate,

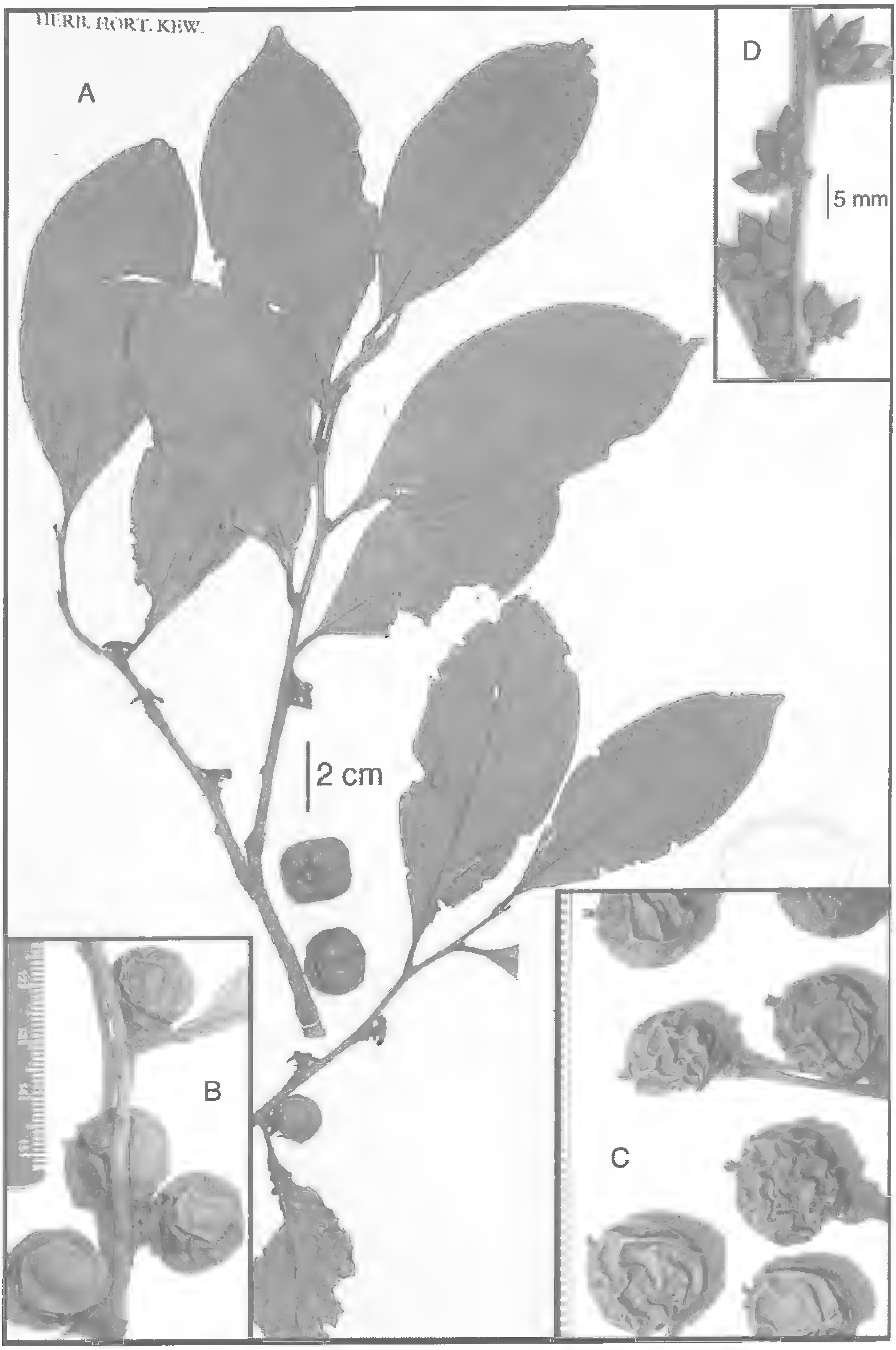

FIG. 8. ***Diospyros hartmanniana*****. A.** Fruiting branchlets with persisting calices (*G. Herrera 5669*, K). **B.** Fruiting inflorescences (*E. Bello 1767*, MO). **C.** Immature fruits (*E. Bello 2442*, MO).

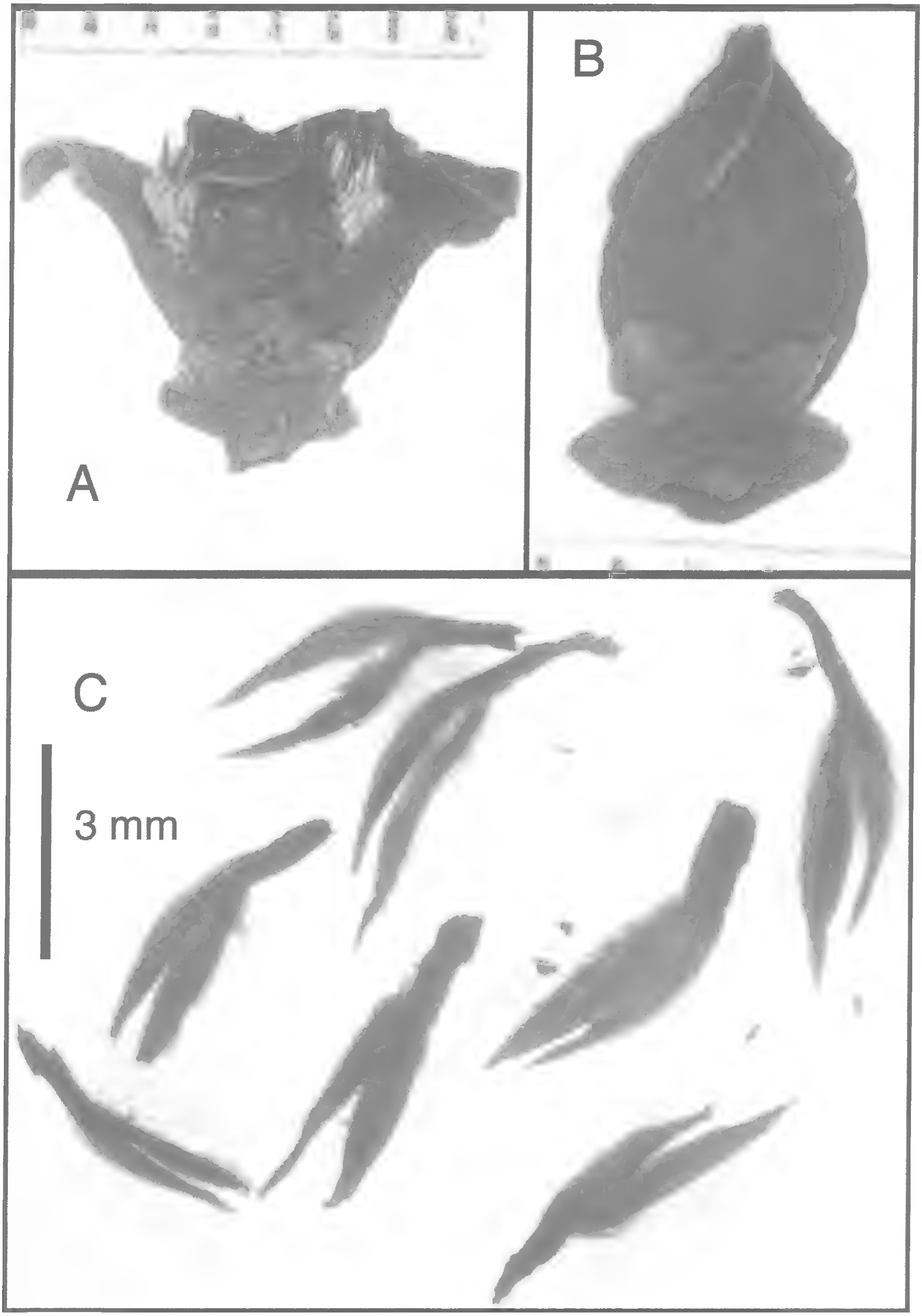

Fig. 9. *Diospyros hartmanniana* (*R. Espinoza et al. 884*, MO). A. Male flower (sinus membranes torn). B. Mature male flower bud. C. Stamens.

1.6–2.8 mm long, 3.2–4.5 mm wide, **lobes** 4–5, widely ovate, 2.1–3.1 mm long, ca. 3 mm wide; **stamens** ca. 27 (based on *R. Espinoza et al. 884* (MO) from Costa Rica) adnate to the base of the corolla, the filaments fused most of their length into ca. 13 pairs, comprised of inner and outer members (Knapp [1997] reports 10–12(–20) stamens, and illustrates 14 stamens in pairs based on *McPherson & Hensold 15303* (MO) from Panama), **anthers** cream, the inner anthers often larger than the outer, lanceolate, (2.5)3–3.2 mm long (including connective), golden to reddish sericeous along the connective on both sides, the apex (connective) rostrate, slightly constricted basally, minutely muricate, **filaments** 1.2–1.5 mm long (fused portion of the filament pair), glabrate, free portion of the filaments 0.5–0.7 mm long, densely hairy, the hairs minute and curly; **pistillode** obturbinate, 1.4 mm high, 1.2 mm wide, ca. 8-lobed/grooved, the 'lobes' narrower than the 'grooves', presence of style-like structures indeterminable due to a dense vestiture of 0.5 mm long, red, flat, twisting hairs in the upper half. **Female inflorescences** unknown with flowers, apparently a 1–3-flowered compact cyme in leaf axils of young stems, with 1–2 fruit developing per inflorescence, axes ± 4-angled, strigillose, with ca. 2 pairs of persistent, widely ovate bracts, 1.2–1.8 mm long, ca. 1.5 mm wide; **fruiting peduncles** 0–1.8 mm long; **fruiting pedicels** 0.5–2 mm long, with a 1–1.5 mm long 4-angled pyramidal apex, the distal 1/2 forming a joint within the basal protuberance of the calyx. **Female flowers** unknown, except **style** divided nearly to the base, branches angled away from one another in the form of a 'V', each 0.7–1.3 mm long, ca. 0.5 mm wide, densely reddish brown strigillose basally and where the style branches diverge (style and stigma [see below] details based on those persisting on fruit), **stigmas** minute, deltoid. **Fruiting calyx** thick, probably fleshy, reportedly brown in life, drying dark brown to black, exterior strigillose, the hairs pale yellow to dark, sometimes glabrescent, epidermis viscid, interior densely strigillose, **tube** patent, with a basal protuberance ca. 1.5 mm long, 5–6 mm wide between opposing sinuses, **lobes** 4–5, spreading, ovate, 2.7–3.8 mm long, (4–)4.4–5.5 mm wide, the margins flat, sparingly ciliate. **Fruit** (14–)17–20 mm long, (12–)17–20 mm wide, depressed globose to subglobose, often appearing 2–4 lobed when dry due to conformation of the fruit wall to the (1–4) locules with developing ovules, usually strigillose basally and at the apex; **flesh** sparse, reddish; **epidermis** smooth to wrinkled, in life orange to orangish red when mature, light brown to dark reddish brown when dry; **seeds** 1–4, loosely contained in the fruit, ± wedge-shaped, reddish brown and rugulose-foveolate textured, though only immature seeds were seen.

Distribution and ecology.—This species is associated with cloud and moist forests between 500 and 2200 m elevation, on slopes of the Cordilleras de Guanacaste and Tilarán in Costa Rica, and Talamanca (La Amistad) in Panama (Fig. 14). Populations occur near, but as far as known do not overlap, populations of *D. haberi* in the former two mountain ranges.

Collections examined. **COSTA RICA. Alajuela. Cantón de San Carlos:** La Fortuna, Finca El Jilguero, 10° 26' 35"N, 84° 41' 25"W, 1140 m, 27 Nov 1992, *G. Herrera 5669* (K). **Cantón de San Ramón:** Res. Biol. Monteverde, Valle del Río Peñas Blancas, Fila de Toro, Sendero Pipilacha y Capo Tres, [acca. W3 Tropicos 10° 18' 00"N, 84° 43' 12"W], 900–1100 m, 21 Jan 1991, *W. Haber (ex E. Cruz) 10632* (MO); Res. Biol. Monteverde, Estación Eladio's, 10° 19'N, 84° 43'W, 820 m, 2 Oct 1990, *E. Bello 2442* (MO). **Cantón de Upala:** P.N. Rincón de la Vieja, Cordillera de Guanacaste, sendero a la Quebrada Mora, camino a la Colonia Blanca, 10° 46' 32"N, 85° 15' 10"W, 840 m, 30 Nov 1990, *G. Rivera 920* (K, MO); P.N. Guanacaste, Cordillera de Guanacaste,, Estación, San Ramón, Dos Ríos, Sector La Campana, 10° 52' 50"N, 85° 24' 05"W, 550 m, 1 May 1993, *R. Espinoza et al. 884* (K, MO); **Guanacaste. Cantón de La Cruz:** De Bahia Salinas a Santa Cecilia Hda. El Oro, 10° 59' 26"N, 85° 25' 40"W, 500 m, 5 Sep 1922, *R. Espinoza 531* (K, MO); **Puntarenas. Cantón de Coto Brus:** Zona Protectora Las Tablas, Cuenca Térraba-Sierpe, 08° 58' 42"N. 82° 50' 14"W, 1500–2000 m, 1 Nov 1996, *A. Rojas & E. Navarro & E. Alfaro 1757* (MO). **Cantón de Osa:** Reserva Biológica Monteverde Quebrada Veracruz, Finca Pablo Morales, 10° 15'N, 84° 48'W, 1600 m, 11 Jan 1990, *E. Bello 1767* (MO); San Luis, Monteverde, Cerro Banquete, camino a Surtubal, 10° 15' 25"N, 84° 47' 20"W, 1100–1200 m, 22 Mar 1994, *Z. Fuentes 704* (MO). **PANAMA. Chiriqui.** Near border with Costa Rica, ca. 13 road km from Río Sereno, Finca Hartmann, 08° 50'N, 82° 45'W, 1400–1800 m, 12 May 1991, *G. McPherson & N. Hensold 15310* (B, 2 sheets, CAS); ridges leading to Cerro Pelota, Parque Nacional Amistad, 08° 52–53'N, 82° 44'W, 1700–2200 m, 21 Aug 2000, *S. Knapp & A. Monro 9254* (MO).

Diospyros juruensis A.C. Smith, Brittonia. 2:163. 1936. (**Figs. 10, 11**). Type: BRAZIL. Amazonas: on varzea land, near mouth of Rio Embira (tributary of Rio Tarauaca), 7° 30'S, 70° 15'W, 26 Jun 1933, B.A. Krukoff 5003 (holotype: NY; isotypes: F, MICH, MO!).

A lengthy description here of the species based on the single sheet with male flowers we have seen seems premature to us. The characters that lead us to believe that *D. juruensis* belongs to the *D. campechiana* complex

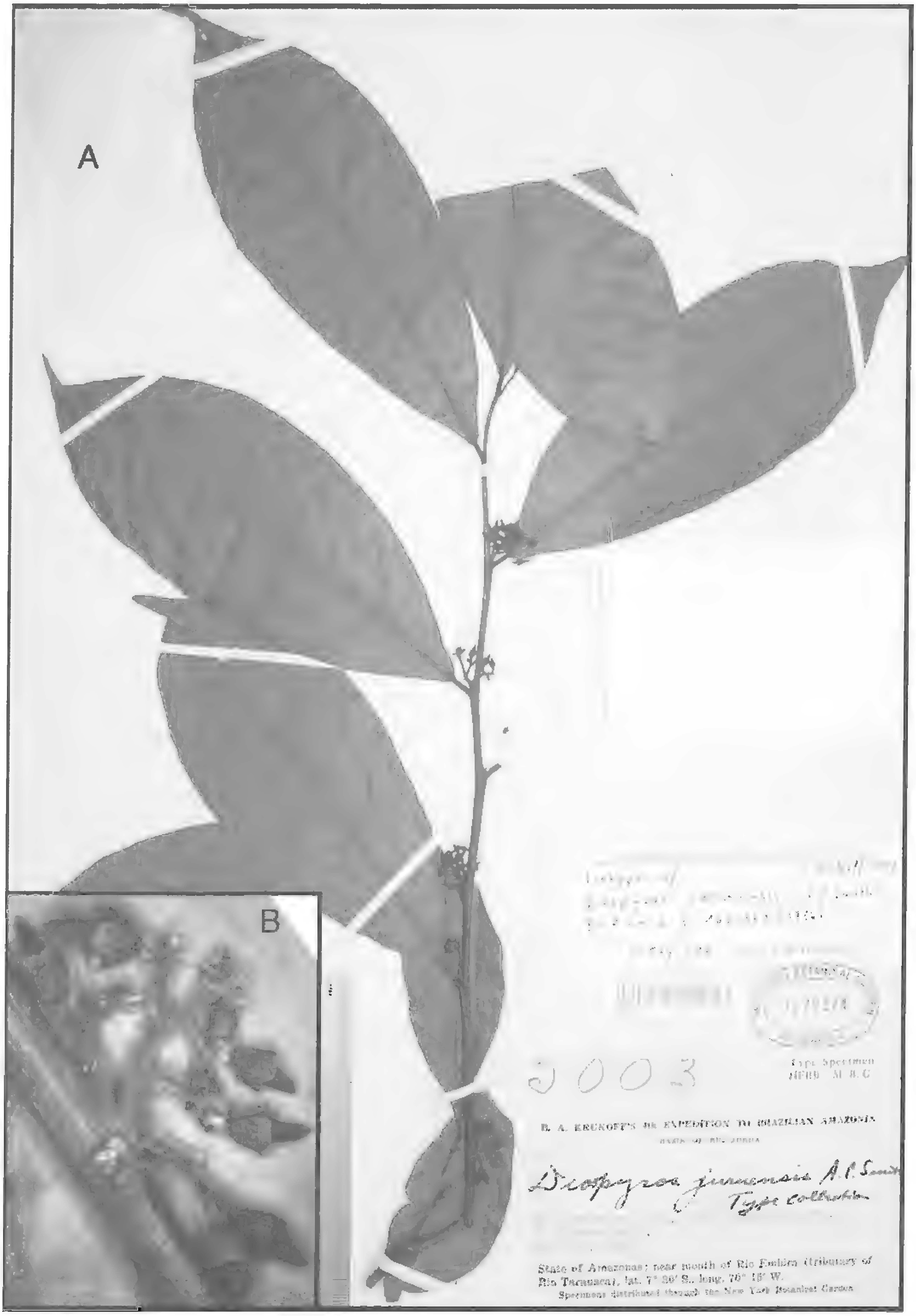

FIG. 10. The isotype of *Diospyros juruensis* (*B.A. Krukoff 5003*, MO). A. Fruiting branchlets with male inflorescences. B. Detail of male inflorescence.

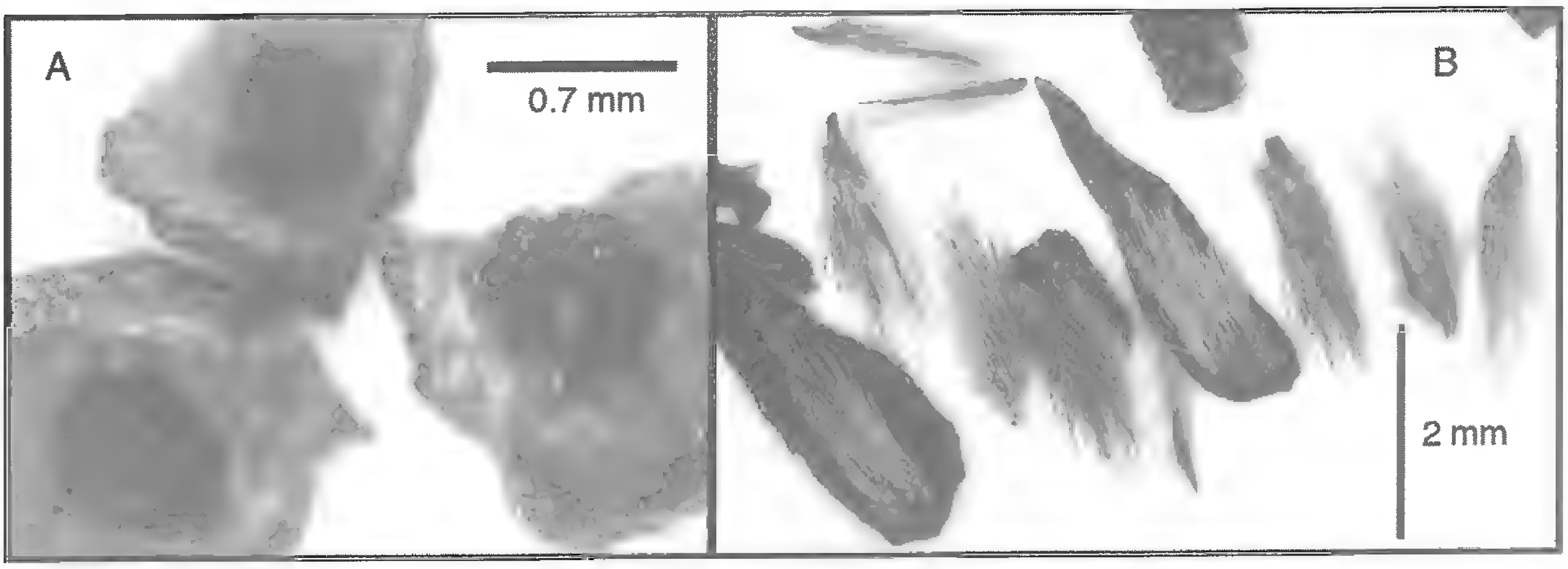

Fig. 11. The isotype of *Diospyros juruensis* (*B.A. Krukoff 5003*, MO). A. Pistillodes. B. Stamens.

include the large oblong-oblanceolate leaves with frequent darkened guard cells and somewhat recessed stomatal apparatus; male inflorescence axes that are markedly 4-angled; depressed orbicular male calyx lobes; a lobed pistillode (Fig. 11a) very similar to that seen in *D. campechiana* (Fig. 3b); stamens adnate to the base of the corolla, fused near the base of their filaments into ca. 16 pairs, outer and inner stamens ± same length, densely golden sericeous on the filament and connective, anthers reddish orange, lanceolate, the apex (connective) tapered and minutely muricate.

Diospyros panamense S. Knapp, Novon 9:524. 1999. (**Figs. 12, 13, 15f**). Type: PANAMA. San Blas: Río Diablo y vecinidad de Duque Sui, a unos 10 km de la costa frente a la Isla de Nargana, ruta hacia Cerro Ibedón, 80–110 m, 09° 22'N, 78° 35'W, [1 Jul 1992 acc. to W3Tropicos], *H. Herrera et al. 1175* (holotype: BM; isotypes: MO, PMA). Replaced name: *Diospyros whitei* S. Knapp, Novon 7:258. 1997. Non *Diospyros whitei* Dows.-Lem. & Pannell, Bull. Jard. Bot. Nat. Belg. 65:399. 1966.

Trees 5–20 m tall, evergreen; **trunk** up to 40 cm dbh, bark black, wood reportedly soft; **young stems** hollow, distally angular, ± compressed and shallowly channeled, terete and smooth proximally, dark, green, brown or gray, occasionally sparsely strigillose, the hairs dark, or sometimes yellowish, minutely pubescent, the hairs colorless, curved-acicular, ca. 0.03 mm long; **mature stems** with thick, scaly, gray to dark brown bark, lenticels prominent, stemwood reddish brown in stems ca. 10 mm wide. **Leaves** alternate, simple, entire; **petioles** 7–14 mm long, subterete, minutely curved-acicular pubescent, epidermis green or atropurpureous, sometimes glaucous and scintillant, sometimes with a few transverse fissures, rounded below, glabrate to sparsely strigillose, ± flattened above, sparsely strigillose, with a densely glandular narrow central channel; **lamina** subcoriaceous to coriaceous, oblong-elliptic to elliptic, though slightly wider in the upper half, (96–)127–240 mm long, 45–107 mm wide, length to width ratio ca. 2–2.6 **:** 1, *base* acute to obtuse, sometimes abruptly decurrent on the petiole, *margin* flat to revolute, *apex* acuminate with a rounded tip; **lower lamina surface** reddish brown, glabrate to sparsely strigillose, faintly papillose, guard cells sometimes dark and recessed; **upper lamina surface** grayish to greenish brown, markedly duller than the lower surface, glabrous to sparsely strigillose near the midrib, epidermis conspicuously papillose, the papillae angular. **Venation** eucamptodromous, subscalariform (*sensu* Knapp 1997), minutely curved-acicular pubescent below; **midrib** prominent below, rounded, glabrate to sparsely strigillose, longitudinally wrinkled, concave above, sparsely to moderately strigillose and glandular; **lateral veins** ± evenly spaced, 6–9 per side, fine below, though prominently raised, barely depressed above, the surface smooth, and so, conspicuous adjacent to the papillate surface of the lamina; **3° veins** fine below, though prominently raised, scarcely, if at all apparent above. **Laminar extrafloral nectaries** on the abaxial surface only, occasional, more frequent near the midrib, dark brown to black, ca. 0.6 mm wide, minutely rimmed. **Male inflorescences** glomerules, or compact cymes, (3–)10–20-flowered, a few at the base of young stems, or solitary in leaf axils, axes 4-angled, dark reddish brown strigillose, subtended by ± 2 strigillose triangular bracts, ca. 0.9 mm long; **peduncles** 0.1–1

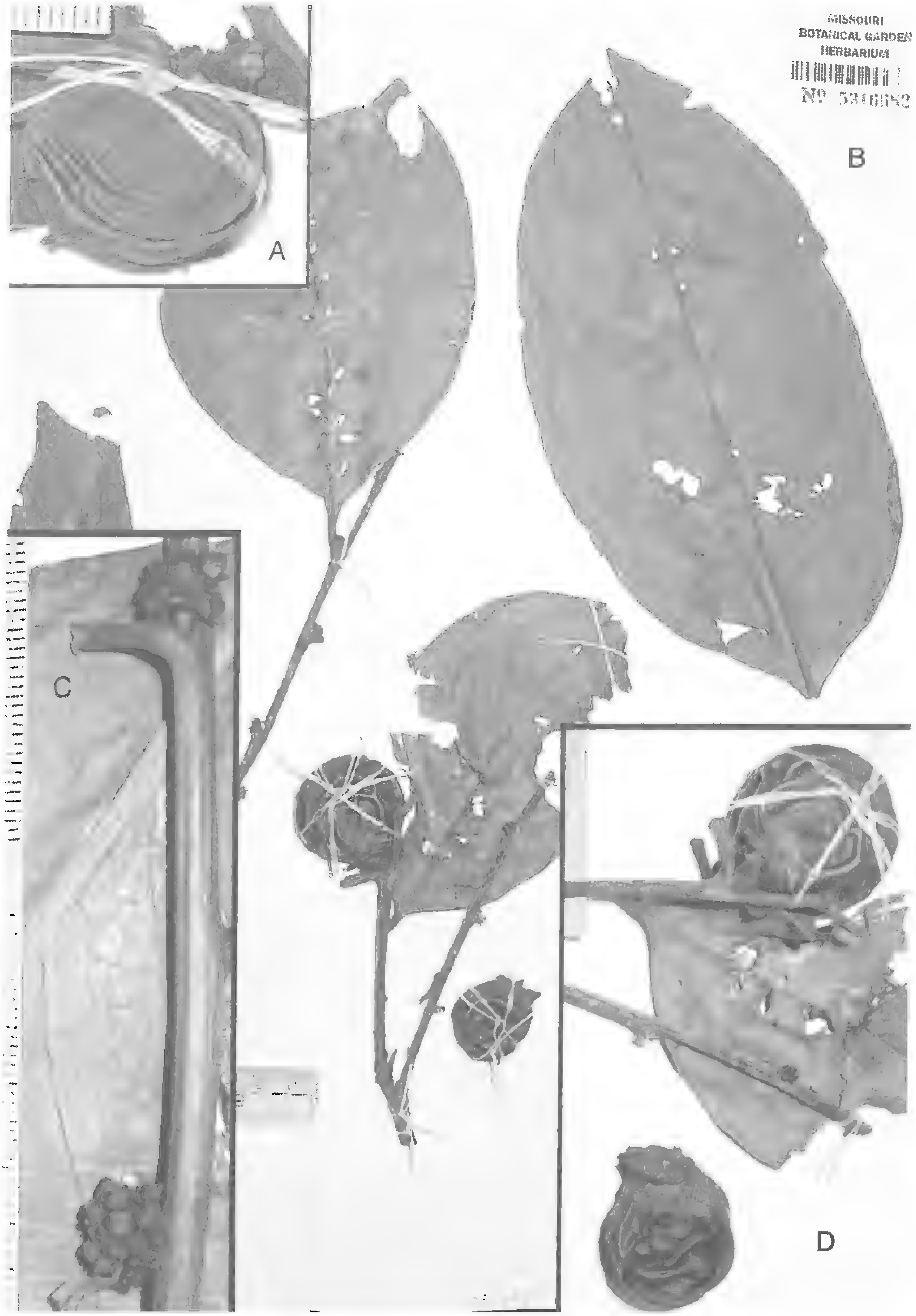

FIG. 12. *Diospyros panamense*. **A.** Immature fruit (*E. Alfaro 291*, MO). **B.** Fruiting branchlets (*R. Aguilar et al. 2727*, MO). **C.** Male inflorescences (*R. Aguilar 2749*, K). **D.** Fruits (*R. Aguilar et al. 2727*, MO).

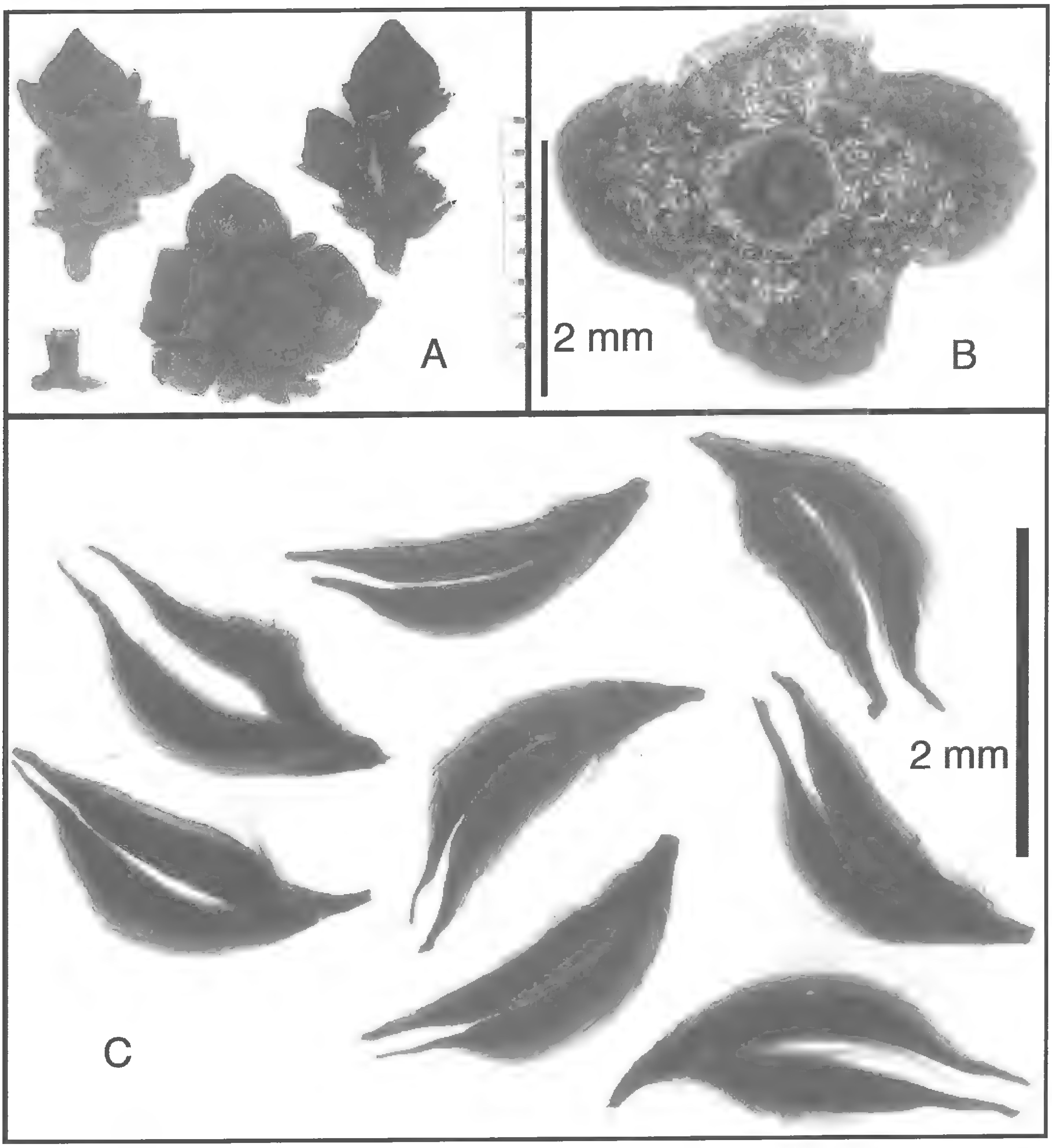

Fig. 13. ***Diospyros panamense*** **(*R. Aguilar 2749*, MO). A. Detail of male inflorescences with flower buds from fragment folder. B. Interior of male calyx with pistillode. C. Stamens.**

mm long; **pedicels** 0–1.4 mm long. **Male flowers** known only from buds; **male flowering calyx** subrotate with a short basal protuberance, exterior drying dark brown to black, strigillose, interior densely strigillose, 3–4.2 mm in widest dimension, **tube** 1–1.5 mm long, **lobes** 4–5, depressed orbicular to ovate, 1–1.6 mm long, 1.8–2.4 mm wide, suberect nearing anthesis; **male corolla** white in life, drying dark brown, thick, glabrous, papillate, **tube** urceolate, 0.8–1.9 mm long, 2.6–3.2 mm wide, **lobes** 4–5, ovate, 1.4–2.2 mm long, 1.6–1.7 mm wide; **stamens** 24–28, adnate to the base of the corolla, fused near the base of their filaments into 12–14 pairs, outer stamens bowing inwards, outer and inner stamens ± same length, the outer stamen golden sericeous abaxially on the filament and connective, the hairs long and curved, also golden sericeous

on the connective adaxially and on both surfaces of the inner stamen, but the hairs shorter, **anthers** reddish orange, lanceolate, ca. 2 mm long, the apex (connective) tapered and minutely muricate, **filaments** 0.2–0.4 mm long; **pistillode** obturbinate, markedly 12–14-lobed, ± 1 mm wide, with 2–3 style-like apical structures, each with a few long straight golden hairs. **Female inflorescences** not seen with flowers, apparently a solitary 1–3-flowered compact fasciculate cyme in the leaf axil of young stems, though no more than one fruit per inflorescence observed, axes 4-angled, sparsely pale strigillose, subtended by several thin, deltoid, strigillose, persistent bracts, ca. 1.5 mm long; **fruiting peduncles** 0–1 mm long; **fruiting pedicels** 1–4 mm long, with a 1–1.2 mm long 4-angled apex, the distal 0.5 mm depressed-pyramidal, forming a joint with the receptacle within the basal protuberance of the calyx. **Female flowers** unknown, except **style** 1.3–1.6 mm long, 0.9–1.3 mm wide, hairy, the hairs pale, yellowish, slightly wavy, terete to slightly 4-angled, bifid, the branches short, 0.2–0.3 mm long, deltoid (style and stigma [see below] details based on those persisting on fruit), **stigmas** depressed orbicular, 0.3 mm long, 0.7 mm wide. Based on the holotype (which we have not seen), Knapp (1997) reported, "styles 5, 1–1.5 mm, fused at the base" and "stigmas irregularly lobed." **Fruiting calyx** thick, possibly fleshy in life, drying dark brown to black, exterior sparsely to densely strigillose, the hairs mostly pale, **tube** patent, with a short protuberance in immature fruit, this apparently absent at maturity, 7–10 mm wide between opposing sinuses, interior densely golden strigillose, **lobes** 4–5, spreading to slightly reflexed, depressed-orbicular, 2.7–5 mm long, 4.5–9 mm wide, the margins sometimes ciliate, interior sparsely golden strigillose. **Fruit** up to 33 mm long, 33 mm wide, globose to subglobose, immature fruit densely hairy near the base and the apex, the remainder sparsely hairy, the hairs golden to dark red, mature fruit glabrous, *locules* probably 1–4, small damaged fruits with ± 2 locules observed, and Whitefoord and Knapp (1998–onward) reporting "lóculos 4?"; **flesh** unknown in mature fruit; **epidermis** mature fruit loosely wrinkled, cracked and scaly near the base and apically, the largest fruits seen (*R. Aguilar 2727 et al.*, MO) reportedly brilliant green; **seeds** unknown. Fruits are suspected to contain up to 4 seeds, though fruits in *E. Alfaro 291* (MO), are probably 1 and 2-seeded based on the number of enlarged locules.

Distribution and ecology.—Lowland rain forests of Costa Rica, Panama, and possibly Columbia, between 80 and 1200 m elevation (Fig. 14). There are reports (Zamora et al. 2004) of this species from both near the highest peaks (617–745 m) and in the low forests (e.g., 0–300 m) on the Osa peninsula. However, we have not seen collections from either of these regions.

Specimens examined. **COSTA RICA. Puntarenas. Canton de Osa:** Fila Costeña, Río Piedras Blancas, junto a la casa, faldas Cerro Anguciana, Fila Cruces. 08° 49' 02"N, 83° 11' 23"W, 900 m, 9 Dec 1993, *R. Aguilar et al. 2727* (MO, K); Fila Costeña, Río Piedras Blancas, cerca de la casa, Cerro Anguciana, Fila Cruces, 08° 49' 02"N, 83° 11' 23"W, 900 m, 10 Dec 1993, *R. Aguilar 2749* (MO, K). **San Jose. Cantón de Perez Zeledon:** Cordillera de Talamanca, La Nubes, Santa Elena, 09° 23' 30"N, 83° 35' 50"W, 1210 m, 3 Aug 1995, *E. Alfaro 291* (MO). **PANAMA. Darien:** Cerro Pirre, 4 Aug 1967, *N. Briston 1229* (MO-2 sheets).

KEY TO THE MESOAMERICAN SPECIES OF THE *DIOSPYROS CAMPECHIANA* COMPLEX

1. Fruits mostly globose to subglobose; plants of Panama and Costa Rica.
   2. Styles 2 or 1 style divided nearly to the base (Fig. 15).
      3. Lamina oblong to oblong obovate; fruiting calyx thin (not fleshy), the lobes 3–4 mm wide, usually reflexed; fruit apex glabrous; styles 0.2 mm thick, erect, glabrous ____ **D. crotalaria**
      3. Lamina elliptic; fruiting calyx thick (fleshy), the lobes 3.8–5.5 mm wide, spreading; fruit apex hairy; styles 0.5–1 mm thick, diverging from near the base in the form of a 'V' to ± erect, hairy or glabrous.
         4. Lamina apex acuminate, upper lamina surface duller and slightly darker than reddish brown lower surface; fruiting calyx lobes 2.7–3.8 mm long, densely dark strigillose inside; style hairy, branches diverging from near the base in the form of a 'V' ____ **D. hartmanniana**
         4. Lamina apex rounded, upper lamina surface shinier and slightly lighter than the greenish to grayish brown lower surface; fruiting calyx lobes 1.5–2 mm long, glabrous inside; style branches glabrous, ± erect (This species typically has one style with some apical notches, or a groove down one side). ____ **D. haberi**
   2. Style 1 (Fig. 15).
      5. Fruiting calyx lobe 2.7–5 mm long, 4.5–9 mm wide; fruiting calyx tube 7–10 mm from sinus to opposite sinus; lamina 96–250 mm long, 45–107 mm wide, the apex acuminate; young stems, petioles, and

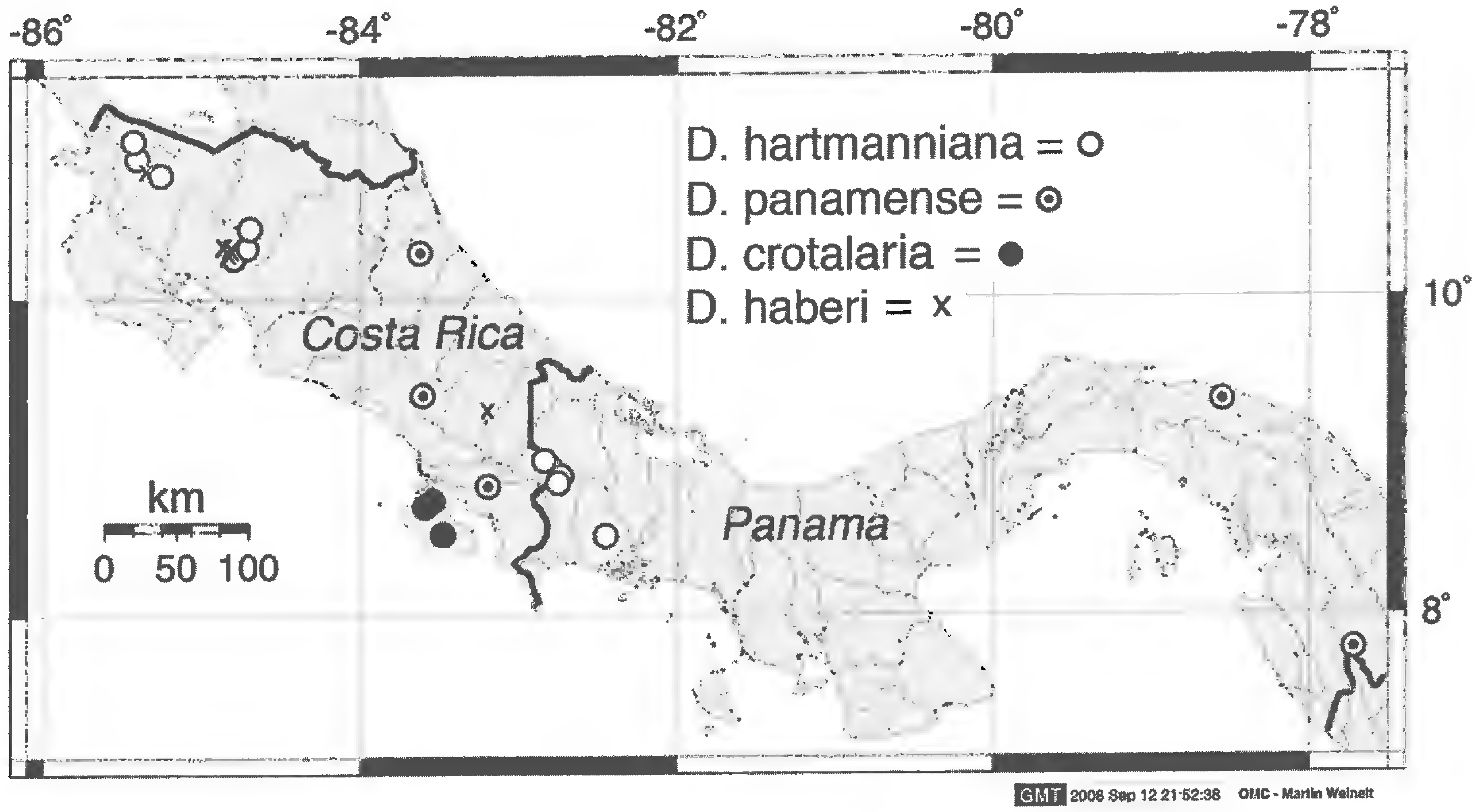

Fig. 14. Distribution of *Diospyros crotalaria, D. hartmanniana, D. haberi* and *D. panamense* in Costa Rica and Panama.

midribs with a sparse, minute, curved-acicular pubescence; fruits up to 32 mm long; style undivided, 1.5–1.6 mm long, 1–1.5 mm thick ____ **D. panamense**

5. Fruiting calyx lobe 1.5–2 mm long, 3.8–5.3 mm wide; fruiting calyx tube 5.1–6.6 mm from sinus to opposite sinus; lamina 30–96 mm long, 17–40 mm wide, the apex rounded; young stems and midribs without a minute curved-acicular pubescence; fruits 14–18 mm long ____ **D. haberi**

1. Fruits mostly ovoid-ellipsoid; plants of Mexico and Guatemala.
   6. Stems, petioles, midribs, and inflorescences minutely hirtellous (in addition to being dark strigillose); fruit 13–17 mm long, the apex glabrous; style 1–2.1 mm long, glabrous; fruiting calyx thin, the tube 3.5–6 mm from sinus to opposite sinus, the lobes 2–4 mm long, not reflexed; lamina 100–285 mm long, oblong to oblong-lanceolate to elliptic, sometimes oblong-oblanceolate, the margins distinctly revolute ____ **D. campechiana**
   6. Stems, petioles, midribs, and inflorescences not minutely hirtellous (dark strigillose only); fruit (15–)18–24 mm long, the apex hairy; style ca. 2.4 mm long, hairy; fruiting calyx thick, the tube 6–7.5 mm from sinus to opposite sinus, the lobes 4–6 mm long, reflexed; lamina 55–152 mm long, widely ovate to elliptic, the margins minutely ridged ____ **D. camposii**

ACKNOWLEDGMENTS

We would like to express our appreciation to Martha L. Orozco-Cardenas at the UCR Plant Transformation Research Center who kindly allowed access to microscopes and photographic equipment. We thank Lia Mansfield for providing Latin translations. Ed Plummer gave much appreciated technical support. We would especially like to extend our gratitude to the following herbaria for specimen loans: B, CAS, CHAPA, F, IJ, K, MO, UCR, UMO, USF, WIS, XAL. Paulo T. Sano and an anonymous reviewer provided helpful comments for improving the manuscript. Finally, we appreciate Giles Waines' continuing support and encouragement of our taxonomic work on the Ebenaceae at the UCR Herbarium.

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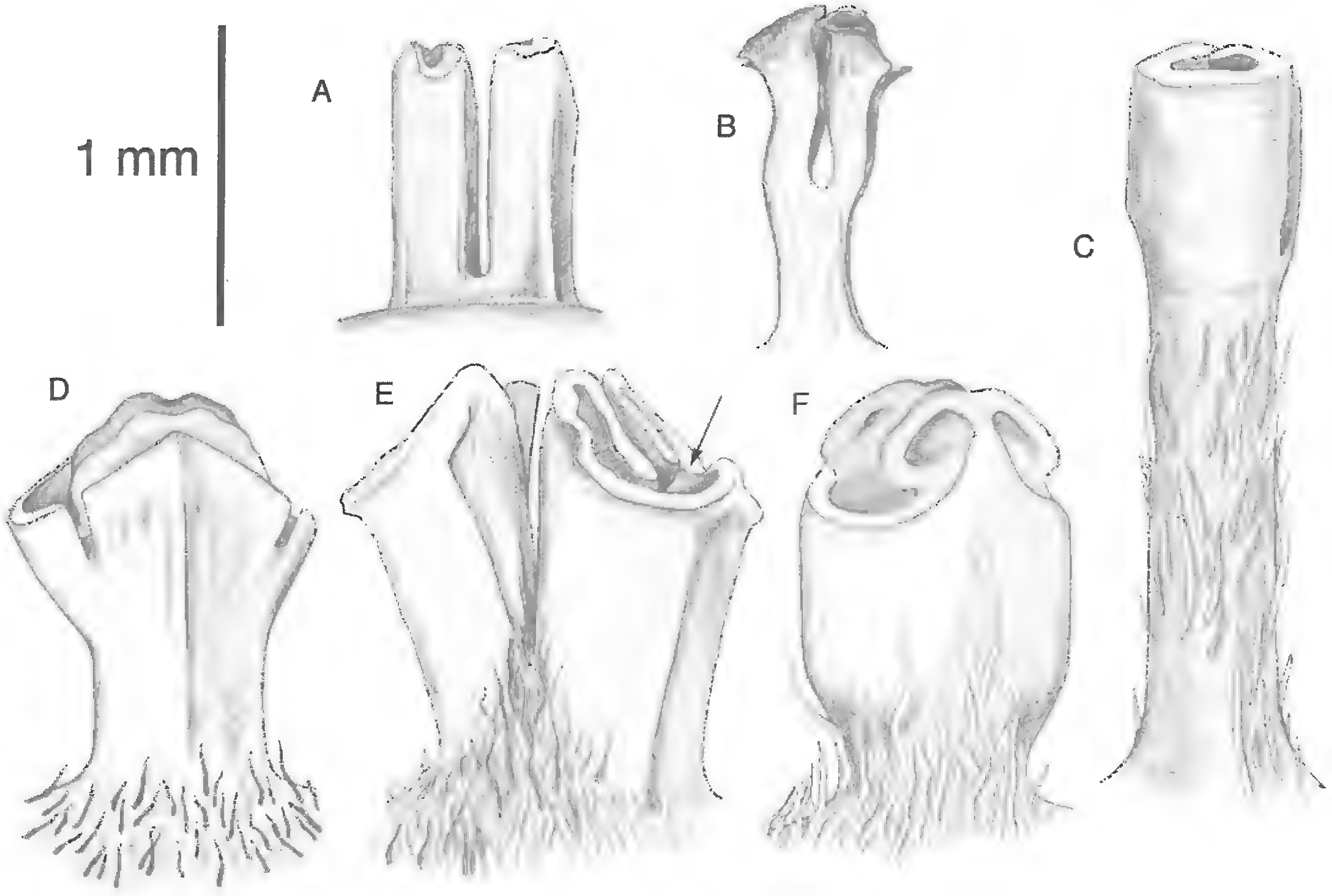

Fig. 15. Stylar variation in the *Diospyros campechiana* complex. A. Styles (with damaged apices) persisting on the fruit apex of *D. crotalaria*, based on the holotype. B. Branched style (with damaged stigmas) of *D. campechiana*, based on *W.E. Harmon & J.E. Fuentes 5790* (UMO). C. Branched style (with damaged apices, and second branch barely visible at this angle) of *D. camposii*, based on the holotype. D. Style with stigmas at fruit apex of *D. haberi*, based on *G. Rivera 1422* (K). E. Styles with minute stigmas (arrow) at the fruit apex of *D. hartmanniana*, based on *E. Bello 2442* (MO). F. Style with stigmas at fruit apex of *D. panamense*, based on *E. Alfaro 291* (MO).

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NOVEDADES Y NOTAS MISCELÁNEAS EN LAS BROMELIACEAE DE MESOAMÉRICA

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RESUMEN

Se describe **Werauhia luctuosa** (Bromeliaceae: Tillandsoideae), una nueva especie de Honduras y se discuten sus afinidades taxonómicas con *W. pittieri*. Adicionalmente, se reporta la presencia de *W. brunei* y *W. camptoclada* en Panamá. Basado en el estudio de especimenes de herbario, material tipo y trabajo de campo, se considera que el material de Mesoamérica previamente identificado como *Aechmea penduliflora* y *Guzmania mitis* (ambas restingidas a Sur América) son actualmente *A. angustifolia* y *G. blasii* respectivamente.

Palabras Clave: Bromeliaceae, Honduras, Costa Rica, Panamá, *Aechmea*, *Werauhia*

ABSTRACT

Werauhia luctuosa (Bromeliaceae, Tillandsoideae), a new species from Honduras is described and its taxonomic affinities with *W. pittieri* are discussed. *Werauhia brunei* and *W. camptoclada* are reported for the first time in Panama. Based on the study of herbarium specimens, type material, and field work, is considered that Mesoamerican material previously identified as *A. penduliflora* and *Guzmania mitis* (both restricted to South America), are actually *A. angustifolia* and *G. blasii* respectively.

Key Words: Bromeliaceae, Honduras, Costa Rica, Panama, *Aechmea*, *Werauhia*

Como resultado de la combinación del trabajo de campo y el estudio de colecciones de herbario tendientes al desarrollo de una Guía de Campo para las Bromeliaceae del Sur de Centroamérica, se proponen la siguiente novedad y notas taxonómicas misceláneas.

Aechmea penduliflora André, Énum. Bromél. 3. 1888. Tipo: COLOMBIA. Santander: Isla Brava, Río Magdalena, entre Yondo y Chucuri, 8 dic 1875, *André 378* (holotipo: K, GH-fotografía).

Distribución.—Colombia y Venezuela a Ecuador y Perú, donde crece en bosques muy húmedos entre los 50 y 700 m.

Aechmea penduliflora ha sido reportada para Nicaragua, Costa Rica y Panamá en diversas ocasiones (Correa et al. 2004; Morales 2003; Utley & Burt-Utley 1994; Utley et al. 2001). Sin embargo, el estudio de su tipo, así como de todos los especimenes citados como testigos en los tratamiento antes mencionados, han revelado que las colecciones (e.g., *Espinoza 94*, INB, MO; *McPherson 8533*, MO; *Rueda & Mendoza 17152*, MO) representan típicos especimenes de *A. angustifolia* Poepp. & Endl. (concordantes en todo sentido con el tipo de este taxón) y que por lo tanto, *A. penduliflora* debe considerarse como una especie no presente aún en Mesoamérica. Esta última especie algunas veces puede tener inflorescencias reducidas, en cuyo caso los ejemplares pueden parecer diferentes de la típica variedad con inflorescencias relativamente largas y elongadas, pero diferentes grados de variación pueden ser observados en el campo, así como en los especimenes de herbario. Esta misma plasticidad en la morfología y tamaño de la inflorescencia está presente en otras especies del genero en Mesoamerica (e.g., *A. tillandsioides* (Schult. f. ex Mart.) Baker).

Guzmania mitis L.B. Sm., Contr. Gray Herb. 98:31, t. 6, f. 4–5. 1932. Tipo: COLOMBIA. Norte de Santander: valle de Pica-Pica, sobre Tapata, al N de Toledo, 1–5 mar 1927 (fl), *Killip & Smith 20195* (holotipo: GH; isotipo: US, INB-fotografía).

Distribución.—Colombia y Venezuela, donde crece en bosques muy húmedos y bosques nubosos entre los 1800 y 2800 m.

En su revisión monográfica de las Bromeliaceae, Smith y Downs (1977) reportó esta especie para Costa Rica, basado en un especimen recolectado por *Foster* en la región de Cartago, lo cual ha sido seguido en forma subsecuente por diversos trabajos florísticos (e.g., Luther 1995; Morales 2003; Utley & Burtley-Utley

1994). Ese especimen corresponde a una ejemplar relativamente pobre, con frutos maduros y carece de flores o incluso brácteas florales completas. El pobre estado de ese especimen fue mencionado anteriormente por Utley y Burtley-Utley (1994). Sin embargo, como resultado del estudio del dicho especimen (*Foster 2686*, US), así como del ejemplar tipo de *Guzmania mitis* y otros especimenes adicionales de esa especie en herbarios de Estados Unidos, Colombia y Venezuela, es claro que la colección colectada por Foster en Costa Rica, fue mal identificada por Smith y Downs (1977) y que en realidad, corresponde a un ejemplar de *Guzmania blassii* Rauh, un taxón similar, pero endémico a Costa Rica. Esta última especie se puede reconocer y separar de *G. mitis* por sus hojas con las láminas con líneas moradas o rojizas longitudinales (vs. concoloras y sin líneas), flores con pedicelos de 4–7 mm de largo (vs. sésiles a subsésiles), pétalos amarillos (vs. blancos) y rangos altitudinales distintos, ya que usualmente *G. blasii* crece en elevaciones entre 700 y 1700 m, mientras que *G. mitis* se encuentra entre los 1800 y 2800 m. Por lo tanto, *G. mitis* debe excluirse como un representante de la flora Mesoamericana y considerarse con un taxón restringido al N de Suramérica.

Werauhia brunei (Mez & Wercklé) J.R. Grant, Trop. Subtrop. Pflanzenwelt 91:31. 1995. *Vriesea brunei* Mez & Wercklé, Bull. Herb. Boissier, ser. 2, 4(9):865. 1904. Tipo: COSTA RICA. San José (citado incorrectamente como Alajuela): Candelaria, oct 1902, *Brune in Werckle Brom. Costar 45* (holotipo: B, INB-fotografía).

Distribución.—Costa Rica y el O de Panamá, donde crece en bosques nubosos y robledales en elevaciones de 1700–2750 m.

Werauhia brunei pertenece a un complejo de especies que se caracterizan por sus inflorescencias simples, las flores siempre con una bráctea adyacente, que usualmente cubre gran parte de los sépalos y con las brácteas variadamente imbricadas (Morales, 2003). Este complejo incluye entre otras a *W. ampla* (L.B. Sm.) J.R. Grant, *W. bicolor* (L.B. Sm.) J.R. Grant, *W. burgeri* (L.B. Sm.) J.R. Grant, *W. gladioliflora* (H. Wendl.) J.R. Grant, *W. macrantha* (Mez & Werckle) J.F. Morales, *W. macrochlamys* (Mez & Wercklé) J.F. Morales, *W. osaensis* (J.F. Morales) J.F. Morales, *W. tiquirensis* (J.F. Morales) J.F. Morales y *W. tonduziana* (L.B. Sm.) J.R. Grant, las cuales en general, son superficialmente similares y de difícil distinción (Morales, 1999, 2003). *Werauhia brunei* se puede separar por sus brácteas florales usualmente dísticas antes y después de la antesis (incluso con frutos maduros), lisas, verdes a verde-canela y de (4.9–)5.2–6 cm de largo. Para mayor información, véase el trabajo de Morales (2003).

Especímenes examinados. **PANAMÁ. Chiriquí:** cerro Punta, falda NO, camino desde Finca Drácula hacia el último lodge dentro del Parque, 10 ago 2006 (fl), *Morales & Santamaría 14625* (INB).

Werauhia camptoclada (Mez & Wercklé) J.F. Morales, Monogr. Syst. Bot. Missouri Bot. Gard. 92:360. 2003. *Vriesea camptoclada* Mez & Wercklé, Repert. Spec. Nov. Regni Veg. 14(400–404):247. 1916. Tipo: COSTA RICA. San José: en las cercanías de La Palma, oct 1908, *Wercklé in Inst. Costaric. 17292* (holotipo: B, INB-fotografía; isotipo: GH).

Distribución.—Costa Rica y el O de Panamá, creciendo en bosques nubosos en elevaciones de 1500–2100 m.

Werauhia camptoclada es una especie distintiva que se puede confundir con *W. moralesii* Luther, *W. kupperiana* (Suess.) J.R. Grant y *W. werckleana* (Mez) J.R. Grant, pero que se puede reconocer por su roseta densa y pequeña (en relación al tamaño de la inflorescencia), hojas que no exceden los 35 cm de largo e inflorescencias con las ramas secundarias que raramente exceden los 12 cm de largo. Esta especie ha sido considerada endémica a Costa Rica (e.g., Morales 2003) pero ahora se conoce en el O de Panamá en las estribaciones de la Cordillera de Talamanca.

Especímenes examinados. **PANAMÁ. Chiriquí:** cerro Punta, falda NO, camino desde Finca Drácula hacia el último lodge dentro del Parque, 10 ago 2006 (fl), *Morales & Santamaría 14626* (INB).

Werauhia luctuosa J.F. Morales, sp. nov. (**Fig. 1**). Tipo: HONDURAS. Santa Bárbara: lago Yojoa, El Sauce, 9 abr 1951 (fl), *L. Williams & A. Molina 17704* (holotipo: EAP, INB-fotografías).

A *Werauhia pittieri* (Mez) J.R. Grant, cui similis, scapo 36–37 cm longo (vs. 45–55 cm), sepalis 3.2–3.5 cm longis (vs. 1.7–2.8 cm) et coma alba (vs. ferruginea) differt.

Plantas acaulescentes, con una altura en floración de 50 a 60 cm. Hojas rosuladas, más o menos erectas,

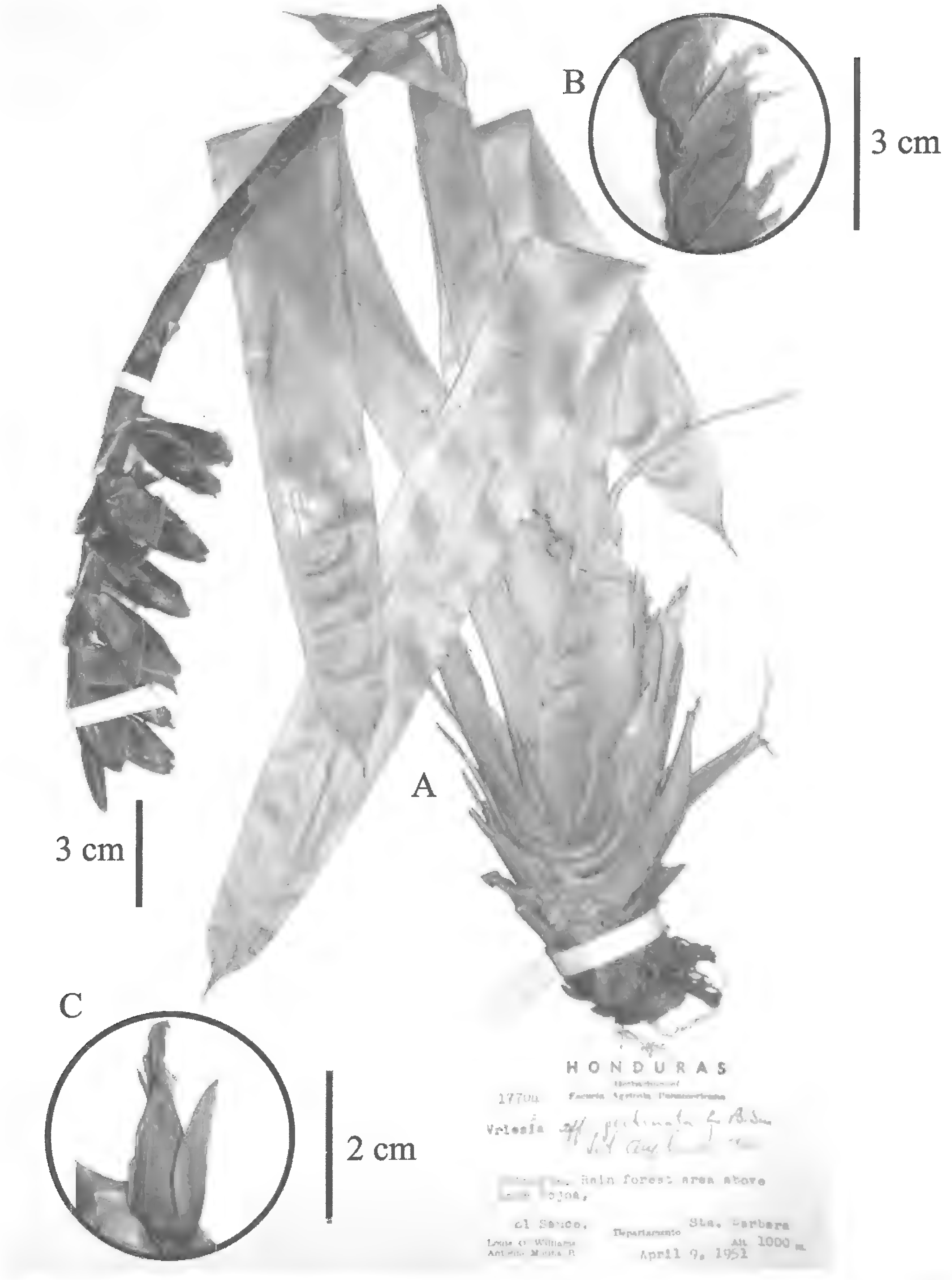

Fig. 1. ***Werauhia luctuosa*** **(del holotipo). A. Planta con inflorescencia. B. Detalle de las brácteas florales. C. Detalle de los sépalos.**

41–46 cm de longitud, densamente punteado-lepidotas en la superficie abaxial, el indumento escaso y más esparcido en la superficie adaxial, delgadas, verdes por ambas superficies; bases de la lámina anchamente elípticas, 9–11 × 4.5–6 cm, pálidas, usualmente concoloras con las láminas, densamente punteado-lepidotas en la superficie abaxial; lámina de las hojas liguladas, abruptamente corto-acuminadas, 31–34.5 × 3.5–4.1 cm. Escapo erecto, 36–37 × 0.5–0.6 cm, diminutamente papilado; brácteas del escapo erectas, 4.3–4.6 cm de longitud, anchamente ovadas, mucho más largas que los internudos, densamente imbricadas, café oscuro basalmente, algo más claras distalmente, sobretodo en la región del ápice, lisas. Inflorescencias erectas, simples, 12–13 cm de longitud; brácteas florales anchamente ovadas, agudas, 3.5–3.8 × 2.9–3.3 cm, relativamente delgadas, ligeramente imbricadas igualando los sépalos en longitud o ligeramente más cortas, café oscuro, los bordes más claros, ecarinadas, lisas. Flores 5 a 6, con los pedicelos de 4–5 mm de longitud, gruesos, erectos, esparcidamente papilados; sépalos 3.2–3.5 cm de longitud, erectos, elípticos, coriáceos, café oscuro. Corola y cápsula desconocidas.

Distribución & habitat.—Endémica a Honduras, donde se conoce solo de la localidad tipo, en bosques húmedos en elevaciones de 900 a 1000 m.

Werauhia luctuosa se encuentra cercanamente relacionada a *W. pittieri* (Mez) J.R. Grant, ya que ambas especies comparten inflorescencias simples, con brácteas florales y flores unilaterales, café oscuro, densamente imbricadas y de 2.6–3.9 cm de largo, pero la primera especie se puede separar por su escapo más corto (36–37 cm vs. 45–55 cm), sépalos más largos (3.2–3.5 cm vs. 1.7–2.8 cm) y frutos con coma blanca (vs. ferrugínea). Adicionalmente, *W. pittieri* es una especie predominante en bosques nubosos y robledales sobre los 2000 m (raramente a 1850 m), mientras que *W. luctuosa* crece en bosques húmedos entre 900 y 1000 m de elevación. *Werauhia luctuosa* solo es conocida por la colección tipo y a pesar de la búsqueda en otros herbarios no fue posible localizar colecciones adicionales. El epíteto de esta especie está dedicado a la memoria de Rosenda Morales y María Ester Padilla, familiares (tías) fallecidos en forma reciente.

AGRADECIMIENTOS

Quiero agradecer a los siguientes herbarios por permitir el estudio de sus colecciones: BR, CR, EAP, F, K, LAGU, MHES, MO, Y, P, U, US. Barry Hammel (MO) amablemente realizó el resumen en inglés. Asimismo, la visita de algunas instituciones fue financiada por el proyecto "Compartiendo tecnología y desarrollando capacidades para la gestión de la biodiversidad en Centroamérica" financiada por el Gobierno de Noruega y ejecutado en forma parcial por el Instituto Nacional de Biodiversidad (INBio)

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UNA NUEVA ESPECIE Y NOTAS MISCELÁNEAS EN EL GÉNERO *OREOPANAX* (ARALIACEAE) EN CENTRO AMÉRICA

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RESUMEN

Como resultado de la revisión de las especies del género *Oreopanax* (Araliaceae) en Costa Rica, Nicaragua y Panamá, se proponen una serie de novedades que incluyen la descripción de una nueva especie, **O. paramicolus,** la redefinición del concepto de otras (*O. nicaraguensis*), rectificación del rango de distribución geográfica para dos taxones (*O. geminatus, O. peltatus*) y el reporte de una especie en Panamá (*O. nubigenus*).

Palabras clave: Centro América, Costa Rica, Panama, Araliaceae, *Oreopanax*

ABSTRACT

As a result of the revision of species of the genus *Oreopanax* (Araliaceae) in Costa Rica, Nicaragua and Panama, several discoveries have come to light. These include a new species, **O. paramicolus,** here described, the need to adjust the concept *O. nicaraguensis,* and the need to adjust the geographical range for three taxa, *O. geminatus, O. peltatus,* and *O. nubigenus,* the latter newly reported for Panama.

Key Words: Central America, Costa Rica, Panama, Araliaceae, *Oreopanax*

Araliaceae es una familia pantropical de plantas, con alrededor de 41 géneros y ca. 1350 especies, distribuidas principalmente en los trópicos (Plunkett et al. 2004). No existen tratamientos monográficos recientes de los géneros del Nuevo Mundo y a nivel de Centroamérica, lo único disponible son sinopsis (Cannon & Cannon 1989) o tratamientos florísticos (e.g., Cannon & Cannon 2001; Standley 1938). La ausencia de trabajos monográficos y la alta variabilidad foliar en algunos géneros (e.g., *Dendropanax*, *Oreopanax*) ha provocado una taxonomía confusa, sobretodo en lo que la correcta aplicación de nombres se refiere. *Oreopanax*, el cual abarca cerca de 80 especies, 24 de ellas presentes en México y Centroamérica (Cannon & Cannon 1989, 2001), tampoco ha escapado de la situación descrita anteriormente, lo que ha traido como consecuencia la incorrecta aplicación del concepto de algunos taxones y datos de distribución incorrectos para otros.

Como resultado de la elaboración del tratamiento de Araliaceae para el Manual de Plantas de Costa Rica, se realizó un detallado estudio taxonómico de las especies de *Oreopanax* presentes en Costa Rica y países aledaños, que incluyó la revisión de especimenes tipo y material en los principales herbarios de Centroamérica, Estados Unidos y Europa. Como resultado, una serie de novedades fueron encontradas, las cuales son descritas o comentadas a continuación. Estas incluyen la descripción de una nueva especie, así como notas misceláneas sobre la incorrecta aplicación del concepto de algunos taxones y la rectificación del rango de distribución geográfica de otros. Algunos datos citados en el manuscrito han sido tomados del tratamiento de Araliaceae para el Manual de Plantas de Costa Rica (Morales et al., datos sin publ.), por lo que pueden diferir de los de otros tratamientos previamente publicados.

Oreopanax geminatus Marchal, Bull. Acad. Roy. Sci. Belgique, ser. 2, 47:91. 1879. Tipo: NICARAGUA. Nueva Segovia: "America Centralis, ad Sajonia," sin fecha (fl), *A. Oersted 7* (holotipo: C).

Distribución.—México, Belice, Honduras y Nicaragua, en elevaciones de 900–1750(–2000) m.

Oreopanax geminatus fue descrita con base en una colección hecha por Oersted en un sitio inespecífico de Centroamérica, con una localidad vaga "Sejovia" (Marchal 1879). Desde entonces, se ha considerado que esta especie está presente en Costa Rica, pues se asume que la localidad tipo corresponde a una localidad en ese país. En general, muchas de las localidades donde recolectó Oersted en Costa Rica son zonas cercanas

al Valle Central, donde se ha conoce relativamente bien la flora. Sin embargo, aunque dicho colector realizó colecciones principalmente en Costa Rica, también recolectó varios centenares de colecciones en Nicaragua entre 1846 y 1848 (Stevens & Montiel 2001). Luego del estudio del especimen tipo de *O. geminatus*, así como del material de esa especie presente en diferentes herbarios de Europa, Estados Unidos y Centroamérica, hemos llegado a la conclusión de que la localidad "Sejonia" probablemente es análoga con el departamento de Nueva Segovia, en el N de Nicaragua, donde *O. geminatus* es una especie relativamente común (R. Abarca, com, pers.). Adicionalmente, este taxón no se recolectado nunca en el S de Nicaragua ni en ninguna otra región de Costa Rica. Por lo tanto, debemos delimitar que *O. geminatus* tiene un rango geográfico que se extiende del S de México al N de Nicaragua, cuya colección tipo, fue recolectada en algún sitio del departamento de Nueva Segovia en Nicaragua y que por el momento, basado en la evidencia suminstrada por especimenes de herbario, no se conoce en Costa Rica.

Oreopanax nicaraguensis M.F. Cannon & Cannon, Ann. Missouri Bot. Gard. 73:482, f. 1–2. 1986. Tipo: NICARAGUA. Jinotega: camino a Aranjuez, Santa Elena, 1–30 nov 1983 (fr), *S. Vega & J. Quesada 197* (holotipo: BM; isotipos: HNMN, MO).

Distribución.—Endémica a Nicaragua, en elevaciones de 100–1300(–1500) m.

En la descripción de *Oreopanax nicaraguensis* Cannon & Cannon (1986) citaron seis especimenes de Nicaragua, cuatro de Costa Rica y uno de Panamá. Desde entonces, se ha manejado un concepto de esta especie que incluye especímenes que crecen casi a nivel del mar (100 m), hasta las zonas más altas de las Cordilleras en Costa Rica y Panamá (3400 m), lo cual ha sido ampliamente seguido en colecciones de herbarios y tratamientos florísticos subsecuentes (e.g., Cannon & Cannon 1989; Cannon & Cannon 2001). Sin embargo, durante el estudio de material para el tratamiento de Araliaceae para el Manual de Plantas de Costa Rica (Morales et al., datos sin publ.), llegamos a la conclusión de que en la descripción original tres especies distintas fueron citadas en los paratipos: *O. nicaraguensis*, a la cual pertenecen todos los especimenes citados de Nicaragua, *O. donnell-smithii* Standl., a la que corresponde la colección de la cordillera de Tilarán en Costa Rica (*Dryer 1360*, F, MO) y la última de ellas, una especie sin describir y restringida a las zonas más altas de la cordillera de Talamanca en Costa Rica y Panamá (descrita en este trabajo). De esta forma, *O. nicaraguensis* debe considerarse un taxón endémico al N de Nicaragua, el cual se encuentra algo relacionado con *O. donnell-smithii*, *O. paramicolus* y *O. striatus* M.J. Cannon & Cannon, pero que se diferencia de este grupo por sus hojas simples, enteras, con la base obtusa o angostamente redondeada, inflorescencias glabras o glabrescentes, las hermafroditas con cabezuelas cortamente pedunculadas, con grupos de 5 a 10 flores por cabezuela y frutos globosos o subglobosos al madurar, de 6–7 mm de largo y con los estilos con más de la mitad inserta dentro de la depresión apical del fruto.

Oreopanax nubigenus Standl., J. Wash. Acad. Sci. 17:315. 1927. Tipo: COSTA RICA. San José: Las Nubes, 21 mar 1924 (fl), *P. Standley 38806* (holotipo: US).

Distribución.—Costa Rica y el O de Panamá, en elevaciones de 1550–2600(–2850) m.

Esta especie era considerada endémica a la Cordillera Central en Costa Rica (Cannon & Cannon 1989) pero es reportada por primera vez para Panamá, donde se conoce en las estribaciones de la Cordillera de Talamanca, en la provincia de Chiriquí. *Oreopanax nubigenus* puede ser confundida con *O. standleyi* A. C. Sm., aún no reportada para Panamá (Correa et al. 2004), pero se diferencia por sus láminas foliares usualmente más pequeñas (6–10(–11.5) × 4–9.5(–11) cm vs. 12–25.5 × 5.5–20 cm), ramitas jóvenes glabras o glabrescentes con el indumento muy esparcido (vs. tomentosas o tomentulosas) e inflorescencias con las flores hermafroditas con 6 a 8 estilos (vs. 10–12).

Especímenes examinados. **PANAMA. Chiriquí:** Cerro Pate Macho, 31 dic 1985 (fr), *de Nevers & Chanley 6689* (MO).

Oreopanax paramicolus J.F. Morales & A. Idárraga, sp. nov. (**Fig. 1**). Tipo: COSTA RICA. San José: cantón de Pérez Zeledón, Cerro de la Muerte, páramo Buena Vista, 19 oct 1993 (fr), *J.F. Morales, N. Zamora, E. Lépiz & V. Ramírez 1890* (holotipo: INB; isotipo: CR).

Fig. 1. *Oreopanax paramicolus*. **A.** Rama con frutos. **B.** Detalle de los frutos.

A *Oreopanax nicaraguensis* M.J. Cannon & Cannon, cui similis, inflorescentia hermaphrodita 15–30-floris, fructus 8–10 mm longus et stylis exsertis, non inmersis differt.

Árbol o arbusto epífito de 2–10 m de altura, las ramitas glabras o glabrescentes y con el indumento inconspicuo. Hojas simples, enteras; lámina 7–22 × 9–21 cm, anchamente ovada a ovado-elíptica, de forma menos común elíptica, el ápice acuminado o agudo, la base usualmente cordada a subcordada, menos comúnmente redondeada a obtusa, glabra, pecíolo 4–20 cm de largo. Inflorescencias usualmente paniculadas, con las ramificaciones evidentes, 12–17 cm de largo, glabras o glabrescentes y con el raquis inconspicuamente puberulento justo antes de las cabezuelas, raramente con algunas secciones tomentulosas (*González et al. 1592*, INB); cabezuelas de las inflorescencias masculinas 8–12 mm de diámetro, con grupos de 15 a 30 flores, las flores con un estilo solitario; cabezuelas de las inflorescencias hermafroditas 5–7 mm de diámetro, con grupos de 4 a 5(6) flores, las flores con 6–8 estilos. Frutos en grupos de 4–6 por cabezuela, ovoides, con un diámetro de 8–10 mm, los estilos casi totalmente exsertos fuera de la depresión apical del fruto.

Distribución, habitat, y ecología.—Restringida a la Cordillera de Talamanca en Costa Rica y el O de Panamá, donde crece en formaciones de robledales (*Quercus* spp., Fagaceae) y páramos, en elevaciones de 2500–3400 m. Floración se produce entre enero y febrero. Fructificación ocurre de enero a marzo, mayo, y de julio a noviembre.

Oreopanax paramicolus ha sido confundida con *Oreopanax nicaraguensis* M.J. Cannon & Cannon, pero se diferencia por sus inflorescencias hermafroditas con mucho más flores (15 a 30 vs. 5–10), frutos de forma diferente y más grandes (ovoides y de 8–10 mm de largo vs. globosos o subglobosos y de 6–7 mm de largo) y estilos casi totalmente exsertos fuera de la depresión apical en el fruto (vs. estilos con más de la mitad incluida). Adicionalmente, *O. paramicolus* crece en robledales y páramos (incluyendo zonas de transición entre ambos ecosistemas), entre 2500 y 3400 m, mientras que *O. nicaraguensis* crece en bosques muy húmedos, entre los 100 y 1300(–1500) m.

Especímenes examinados. **COSTA RICA. Cartago:** Cerro de la Muerte, La Georgina, 2 ago 1965 (fr), *Croat 261* (MO); reserva forestal Río Macho, estación Ojo de Agua, 12 ene 1996 (fr), *Gamboa & Picado 950* (INB, MO); reserva forestal Río Macho, Cerro de la Muerte, 6 sep 1996 (fr), *Rodríguez et al. 1470* (INB). **Limón:** parque nacional Chirripó, 15 feb 1983 (fl), *Garwood et al. 1273* (BM, MO); parque internacional La Amistad, Tararia, 12 abr 2002 (fr), *González et al. 1592* (INB). **Puntarenas:** Cordillera de Talamanca, Cerro Echandi, 23 ago 1983 (fr), *Davidse et al. 23876* (MO); parque internacional La Amistad, Cerro Echandi, 13 ago 1997 (fr), *Quesada et al. 1994* (INB). **San José:** entre Canaán y Chirripó vía Los Angeles, sobre el Río Talari, 19–22 ene1970 (fr), *Burger & Liesner 7381* (F, MO), 24 ago 1971 (fr), *Burger 8328* (F, MO); parque nacional Chirripó, sendero Paso de los Indios, 1 may 1997 (fr), *Gamboa & Aguilar 1271* (INB) reserva forestal Los Santos, camino a Providencia, 19 jul 1997 (fr), *Gamboa 1620* (INB); Pérez Zeledón, albergue Cuerecí, 8 jul 2000 (fr), *Miller 38* (INB, MO); Salsipuedes, 10 mar 1994 (fr), *Ramírez & Hammel 287* (INB, MO). **San José-Cartago:** Cordillera de Talamanca, Cerros Cuerecí, 15 set 1983 (fr), *Davidse 24705* (MO); Copey, cerro Las Vueltas, 28 Mar 1994 (fr), *Vargas et al. 1748* (CR). **PANAMA. Bocas del Toro:** cerro Fábrega entre cerros Itamut y Bine, Mar 1984 (fr), *Gómez et al. 22461* (MO). **Chiriquí:** Boquete, camino a Volcán Barú, 18 may 1976 (fr), *Croat 34885* (MO); Potero Muleto, Volcán Barú, 27 nov 1975 (st), Volcán de Chiriquí, 20 nov 1975 (fr), *Davidse & D'Arcy 10273* (MO); El Volcán, SE de la Nivera, sin fecha (fr), *D'Arcy 12505* (MO); Volcán Barú, Potrero Muleto, 6 nov 1978 (fr), *Hammel 5642* (MO); Volcán Barú, 24 jul 1975 (fr), *Mori & Bolten 7440* (MO); parque nacional Volcán Barú, 15 ene1992 (fl), *Vega & Rincón* (MO, PMA).

Oreopanax peltatus Linden, Gartenflora 11:170, t. 363. 1862. Tipo: MÉXICO: Datos perdidos, *J. Linden s.n.* (holotipo: BR? n.v.).

Distribución.—México, Guatemala y El Salvador, en elevaciones de 700–1900(–2400) m.

Algunos especimenes de Costa Rica y Panamá, han sido identificados como esta especie (e.g., *Liesner et al. 15518*, MO), pero estas colecciones en realidad corresponden a especimenes de *Dendropanax* estériles, género en el cual la presencia de hojas peltadas e irregularmente lobuladas es algo común en los brotes inmaduros de muchas especies, las cuales se tornan no peltadas con la edad. En Centroamérica *Oreopanax peltatus* se puede reconocer fácilmente por sus hojas simples, 5–7-lobuladas, peltadas y con la base redondeada o subcordada a no peltatas y cordadas e inflorescencias con las flores estaminadas de 3–6 mm de diámetro.

AGRADECIMIENTOS

Deseamos reconocer a los siguientes herbarios por permitir el ingreso a sus colecciones: BM, BR, CGE, COL,

CR, CUVC, F, G, HUA, HUQ, INB, JAUM, K, MEDEL, MA, MO, NY, P, Q, QCA, QCNE, TULV, U, W, WAG. Esta investigación fue posible además gracias al convenio de cooperación entre el Ministerio de Ambiente y Energía (MINAE) y el Instituto Nacional de Biodiversidad (INBio) con el fin de completar el Inventario Nacional de Biodiversidad en Costa Rica.

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BOOK REVIEW

Jules G. Evans. 2008. **California Natural History Guides: Natural History of the Point Reyes Peninsula, Second Edition.** (ISBN 978-0-520-25467-1, pbk.). University of California Press, 2120 Berkeley Way, Berkeley, California 94704-1012, U.S.A. (**Orders:** The University of California Press c/o California/Princeton Fulfillment Services, 1445 Lower Ferry Road, Ewing, New Jersey 08618, U.S.A.; www.ucpress.edu, email orders@cpfsinc.com, 1-800-777-4726, 1-800-999-1958 fax). $24.95, 366 pp, numerous figures, graphs, images, maps, tables, checklists, index, and references, 5 1/4" × 8".

Natural History of the Point Reyes Peninsula is divided into seven sections that specifically describe the climate, geology, and various fauna (e.g. birds, insects, marsupials, carnivores, pinnipeds, bats, whales, ungulates, reptiles, amphibians) and flora communities that inhabit this Californian peninsula. Since the earlier publications of this book (1989, revised 1993), a team of researchers have conducted studies on Point Reyes, and the information they accumulated has greatly enhanced this new edition.

Evans provides a very detailed account of the life that thrives within the ecosystem of Point Reyes. Images of the spectacular scenery and its various inhabitants accompany comprehensive information about each of the region's habitats (terrestrial, riparian, freshwater and marine). Where ever he can, the author sprinkles in historical asides of a particular item, personal anecdotes, and definitions, greatly enhancing the overall reader experience.

I found this book to be very informative and a good resource for any naturalist or person that is eager to learn more about the diversity of biota found on Point Reyes Peninsula, California. The book's size and weight make it an ideal companion for any hiker or outdoorsman. The author used easy-to-understand terms and provided the reader with common and scientific names for most species. The inclusion of a comprehensive checklist of the fauna and flora with information on whether the species is listed as endangered, vulnerable, rare, or threatened further enhanced this book.—*Keri McNew, MS Biology, Programs Manager, Botanical Research Institute of Texas, 500 E 4th Street, Fort Worth, TX 76102, U.S.A.*

FIVE NEW SPECIES OF MYRTACEAE FROM ECUADOR

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ABSTRACT

Five new species of Myrtaceae from Ecuador are described and illustrated: **Calyptranthes compactiflora, C. fusca, C. sparsiflora, Myrcia aequatoriensis,** and **M. verticillata.**

RESUMEN

Se describen y se ilustran cinco especies nuevas de Myrtaceae del Ecuador: **Calyptranthes compactiflora, C. fusca, C. sparsiflora, Myrcia aequatoriensis** y **M. verticillata.**

INTRODUCTION

Among the Myrtaceae from Ecuador, there are approximately 30 species of *Calyptranthes* and ca. 40 species of *Myrcia*, including many new taxa (Holst 1999; Kawasaki & Holst 2005; Holst & Kawasaki 2006, 2008). In preparation of the Myrtaceae treatment for the Flora of Ecuador, five additional new species of these genera are herein described: *Calyptranthes compactiflora*, *C. fusca*, *C. sparsiflora*, *Myrcia aequatoriensis*, and *M. verticillata*.

Calyptranthes compactiflora M.L. Kawasaki & B.K. Holst, sp. nov. (**Fig. 1**). Type: ECUADOR. Sucumbíos (Napo on label): downstream Río Cuyabeno from Laguna de Cuyabeno to Puerto Bolívar, 00°03'S, 76°10'W, 250 m, 14 Apr 1980 (bud), *J. Brandbyge, E. Asanza & L. Reib 30543* (holotype: AAU; isotypes: F, QCA, SEL).

Arbor, indumento rufo-brunneo, ferrugineo vel flavo-brunneo; ramulis teretis; foliis anguste ellipticis vel ellipticis, chartaceis, 5–8 × 1.8–3 cm, abrupto-acuminatis, siccatis atrobrunneis; paniculis valde abbreviatis, compactifloris; alabastris clausis 3–4 mm longis.

Tree ca. 4 m tall, the trichomes dibrachiate, reddish-brown, ferrugineous to yellowish-brown; branchlets terete, appressed-pubescent. **Leaf blades** narrowly elliptic to elliptic, chartaceous, 5–8 × 1.8–3 cm, the upper surface drying dark-brown, glabrous and lustrous, indistinctly or impressed-punctate, the lower surface reddish-brown in drying, sparsely appressed-pubescent, distinctly dark-punctate; midvein impressed above, convex below; lateral veins 35–40 pairs, parallel, scarcely raised on both surfaces; marginal vein 1, ca. 1 mm from the margin, equaling the lateral veins in prominence; apex abruptly acuminate, the acumen to ca. 1.3 cm long; base cuneate; petioles 5–9 mm long, channeled, puberulous, blackish. **Inflorescences** of paired, very abbreviate panicles appearing glomerulate by the reduction of the main axes, axillary, with up to ca. 6 flowers, the peduncle 1–2(–10) mm long, pubescent; bracts lanceolate, 3–5 mm long, appressed-pubescent, early deciduous; bracteoles ovate, ca. 2 mm long, appressed-pubescent, deciduous. **Flowers:** buds closed, obovoid, 3–4 mm long, sessile, appressed-pubescent, glabrescent, the hypanthium furfuraceous, yellowish-white; calyptra obtuse to shortly apiculate, sparsely pubescent; petals absent; disk ca. 2 mm diam., glabrous; stamens numerous, ca. 2–3 mm long, the anthers ca. 0.5 mm long; style ca. 2 mm long; ovary 2-locular; ovules 2 per locule. **Fruits** not seen.

Distribution.—Known only from the type collection from northeastern Ecuador in the Río Cuyabeno region, in riverside forests at 250 m elevation.

Calyptranthes compactiflora is readily recognized by the greatly reduced inflorescences, also seen in *C. smithii* McVaugh, a species known only by the type collection from Guyana. These two species may be distinguished by leaf characters: in *C. compactiflora*, the leaves are chartaceous, 5–8 × 1.8–3 cm, the midvein

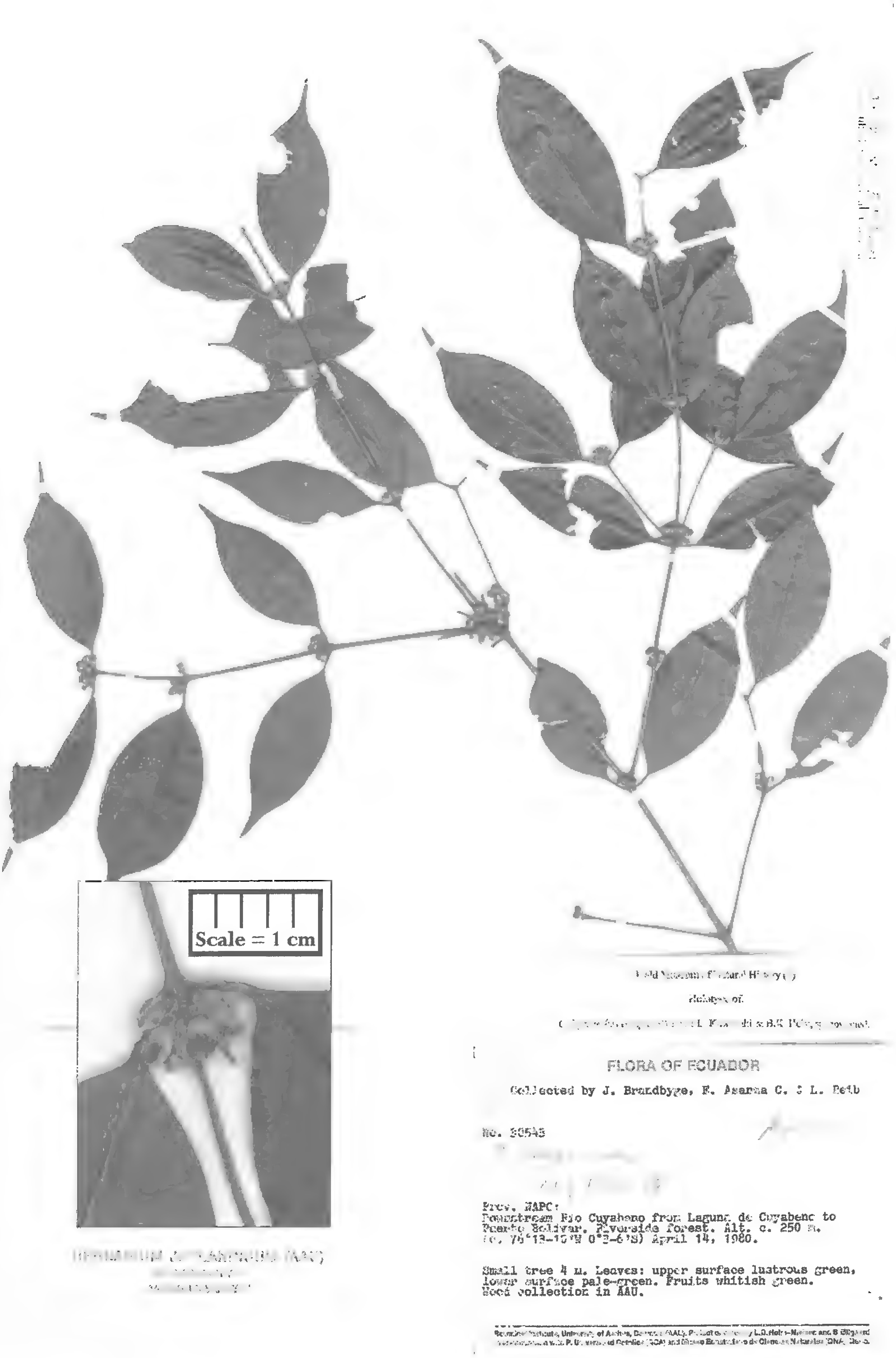

Fig. 1. *Calyptranthes compactiflora* M.L. Kawasaki & B.K. Holst (*Brandbyge et al. 30543*: Holotype, AAU; inset from isotype at SEL).

is clearly impressed above, and the petioles are 5–9 mm long; in *C. smithii*, the leaves are coriaceous, 9–12 × 3.5–4.5 cm, the midvein is plane to impressed above, and the petioles are 10–13 mm long.

Calyptranthes fusca M.L. Kawasaki & B.K. Holst, sp. nov. (**Fig. 2**). TYPE: ECUADOR. CARCHI: Tulcán Cantón, Parroquia Tobar Donoso, Sector Sabalera, Reserva Indígena Awá, 01°00'N, 78°24'W, 650–1000 m, 19–28 Jun 1992 (fl), *G. Tipaz, J. Zuleta & N. Guanga 1438* (HOLOTYPE: QCNE; ISOTYPES: F, MO, SEL).

Arbor, indumento flavescenti; ramulis teretis; foliis anguste ellipticis, ellipticis vel oblanceolatis, chartaceis, 5.5–14 × 3–5 cm, abrupto-acuminatis, siccatis atrobrunneis; paniculis paucifloris; alabastris 1–3 mm longis, petalis nullis; baccis globosis, atropurpureis.

Tree 10–20 m tall, 15–40 cm dbh, the trichomes dibrachiate, yellowish; branchlets terete, puberulous. **Leaf blades** narrowly elliptic to elliptic, or oblanceolate, chartaceous, 5.5–14 × 3–5 cm, drying dark-brown to brownish above, paler below, glabrous on the upper surface, sparsely appressed-pubescent to glabrous on the lower surface, the trichomes located especially along venation; glands distinctly dark-brown, plane above, salient below, also on venation, branchlets, and inflorescences; midvein impressed above, convex below; lateral veins 10–15 pairs, impressed above, salient below; marginal veins 2, the innermost arched, 3–5 mm from the margin, similar to the lateral veins in prominence, the outermost less prominent, parallel to the margin, ca. 1 mm from it; apex abruptly acuminate, the acumen 1–1.5 cm long; base cuneate to obtuse; petioles 5–10 mm long, channeled, sparsely pubescent, blackish. **Inflorescences** of paired panicles, subterminal or axillary, with up to ca. 20 flowers, 2–8 cm long, the branches densely appressed-pubescent, gland-dotted; bracts ovate, ca. 2 mm long, puberulous, early deciduous; bracteoles lanceolate, ca. 1 mm long, puberulous, deciduous. **Flowers:** buds closed, obovoid to subglobose, of very different sizes, 1–3 mm long, sessile, the lateral flower buds of the terminal triads apparently abortive; hypanthium prolonged ca. 1 mm beyond the ovary, glabrous; calyptra obtuse to minutely apiculate, glabrous; petals absent; disk ca. 2 mm diam., glabrous; stamens numerous, ca. 4–5 mm long, the anthers ca. 0.3 mm long; style ca. 5 mm long; ovary 2-locular; ovules 2 per locule. **Fruits** berries 1–2 cm diam., globose, crowned by the hypanthium scar, dark-purple, glabrous, prominently gland-dotted, the pericarp thick and hard; seed 1, ca. 9 × 7 mm, the seed coat membranous; embryo myrcioid, the cotyledons leafy and folded, the radicle elongate, equaling the cotyledons in length.

Distribution.—Known from several collections from northwestern Ecuador of the same area (Reserva Etnica Awá) in the provinces of Carchi and Esmeraldas, in humid, lowland to premontane forests at 200–1600 m elevation. The wood is utilized for ax handles and other tools (*Tipaz et al. 1290*) and the edible fruits to cure diarrhea (*Tipaz et al. 1233*). Common names are recorded as "ungal nusma" (*Tipaz et al. 1290*), "unga lusma" (*Tipaz et al. 1438*), and "pishuilde" (*Tipaz et al. 1126*).

The leaves of *Calyptranthes fusca* and *C. cuspidata* DC., a species from Amazonian Brazil and Peru, are morphologically similiar and dark-brown in drying. *Calyptranthes fusca* is distinguished from *C. cuspidata* by having the leaves with impressed (vs. convex) midveins above, conspicuous (vs. inconspicuous) and dark glands on both surfaces, along the venation and on the inflorescence axes, and relatively few-flowered (vs. multiflorous) panicles. The varying size of the flower buds is unusual in the family.

Additional collections examined: **ECUADOR. Carchi:** Maldonado, Parroquia Tobar Donoso, Reserva Etnica Awá, Sabalera, 00°55'N, 78°32'W, 900 m, 22 Nov 1992 (fr), *C. Aulestia et al. 658* (F, MO, QCNE, SEL). Tulcán Cantón, Parroquia Tobar Donoso, Sector El Baboso, Reserva Indígena Awá, 00°53'N, 78°00'W, 1600 m, 3 Oct 1991 (fr), *G. Tipaz et al. 310* (F, MO, QCNE, SEL). Tulcán Cantón, Parroquia Chical, Sector Gualpi medio, Reserva Indígena Awá, 01°02'N, 78°16'W, 1000 m, 23–27 May 1992 (fr), *G. Tipaz et al. 1126* (F, MO, QCNE, SEL). Tulcán Cantón, Parroquia Tobar Donoso, Sector Sabalera, Reserva Indígena Awá, 01°00'N, 78°24'W, 650–1000 m, 19–28 Jun 1992 (fr), *G. Tipaz et al. 1233* (F, MO, QCNE, SEL). Tulcán Cantón, Parroquia Tobar Donoso, Sector Sabalera, Reserva Indígena Awá, 01°00'N, 78°24'W, 650–1000 m, 19–28 Jun 1992 (fl), *G. Tipaz et al. 1290* (F, MO, QCNE, SEL). **Esmeraldas:** San Lorenzo Cantón, Parroquia Mataje, Reserva Etnica Awá, Centro Mataje, on the banks of Río Mataje, 01°08'N, 78°33'W, 200 m, 21 Sep 1992 (fr), *C. Aulestia et al. 551* (F, MO, QCNE, SEL). San Lorenzo Cantón, Parroquia Mataje, Reserva Etnica Awá, Centro Mataje, on the banks of Río Mataje, 01°08'N, 78°33'W, 200 m, 21 Sep 1992 (fr), *C. Aulestia et al. 568* (F, MO, QCNE, SEL).

Calyptranthes sparsiflora M.L. Kawasaki & B.K. Holst, sp. nov. (**Fig. 3**). TYPE. ECUADOR. SUCUMBÍOS: Lago Agrio Cantón, Reserva Cuyabeno, Laguna Canangueno, 00°02'S, 76°13'W, 230 m, 18 Nov 1991 (fl), *W. Palacios, G. Tipaz, D. Rubio, E. Gudiño & C. Aulestia 9126* (HOLOTYPE: QCNE; ISOTYPE: MO, SEL).

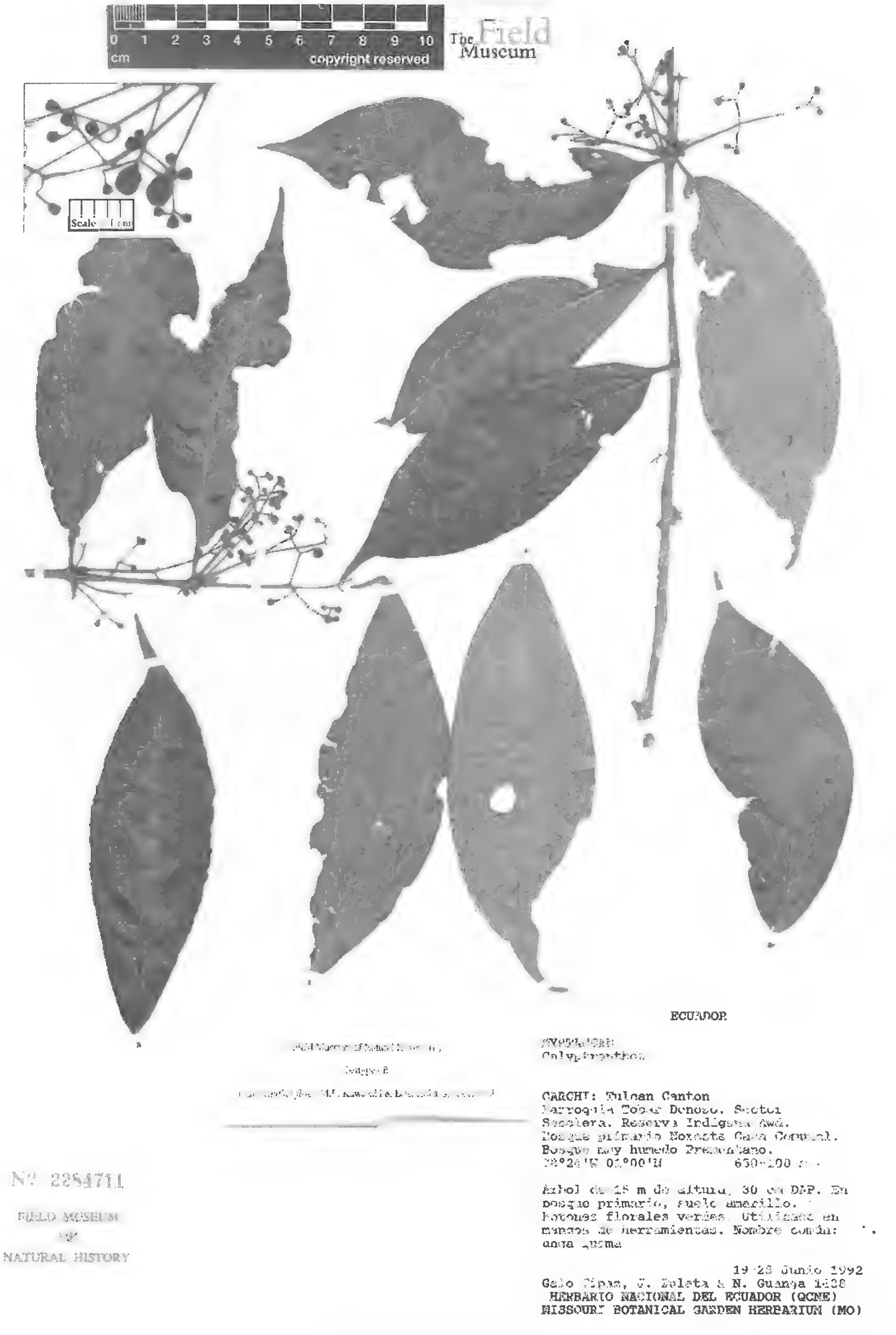

Fig. 2. *Calyptranthes fusca* M.L. Kawasaki & B.K. Holst (*Tipaz et al. 1438*: Isotype, F; inset from isotype at SEL).

FIG. 3. *Calyptranthes sparsiflora* M.L. Kawasaki & B.K. Holst (*Palacios et al. 9126*: Isotype, MO; inset from isotype at SEL).

Frutex vel arbor, indumento rufo-brunneo; ramulis carinatis; foliis anguste ellipticis, chartaceis, 4–6.5 × 1.5–2.5 cm, caudato-acuminatis; inflorescentiis 1 vel 3 floris, dense appresso-pubescentibus; baccis globosis.

Shrub or tree 1.5–4 m tall, the trichomes dibrachiate, reddish-brown, to 0.5 mm long; branchlets bicarinate, thinly appressed-pubescent to glabrous. **Leaf blades** narrowly elliptic, chartaceous, 4–6.5 × 1.5–2.5 cm, the upper surface drying olive-green to dark-brown, glabrous, indistinctly or impressed-punctate, the lower surface light-brown in drying, sparsely appressed-pubescent, minutely punctate; midvein impressed above, convex below; lateral veins 30–40 pairs, parallel, scarcely raised on both surfaces; marginal vein 1, 0.5–1 mm from the margin, equaling the lateral veins in prominence; apex caudate-acuminate, the acumen to ca. 1.5 cm long; base obtuse to cuneate; petioles 1–3 mm long, channeled, puberulous. **Inflorescences** paired, subterminal, with 1 or 3 subsessile flowers, borne at the end of a 1.3–2.8-mm long peduncle, densely appressed-pubescent; bracts and bracteoles early deciduous, not seen. **Flowers:** buds not seen, the hypanthium 1.5–2 mm long, densely appressed-pubescent; calyptra ca. 1 mm long, shortly apiculate, densely to loosely appressed-pubescent; petals not seen; disk ca. 2 mm diam., glabrous; stamens not seen expanded, the anthers ca. 0.3 mm long; style ca. 7 mm long. **Fruits** berries, immature, globose, 8–9 mm diam., yellow, appressed-puberulous, the trichomes located especially at the base and by the hypanthium scar; seed 1, ca. 8 × 7 mm, the seed coat membranous; embryo myrcioid, the cotyledons leafy and folded, the radicle elongate, equaling the cotyledons in length.

Distribution.—Known from eastern Ecuador in Sucumbíos and Pastaza provinces, in primary rain forests at 200–230 m elevation.

Calyptranthes sparsiflora is characterized by the very reduced, 1- or 3-flowered inflorescences, that are densely appressed-pubescent with reddish-brown trichomes. Among the species from Ecuador, it resembles *C. bipennis* O. Berg on branchlet, leaf, and inflorescence morphology. These two species may be distinguished by the presence of indumentum on young vegetative growth, leaves, inflorescences, flowers, and fruits in *C. sparsiflora* (vs. mostly glabrous in *C. bipennis*).

Additional collection examined: **ECUADOR. Pastaza:** Lorocachi, SW of the military camp, 01°38'S, 75°58'W, 200 m, 26 May 1980 (fr), *J. Jaramillo et al. 31106* (AAU, F, QCA).

Myrcia aequatoriensis M.L. Kawasaki & B.K. Holst, sp. nov. (**Fig. 4**). Type: ECUADOR. Sucumbíos: Reserva Faunística Cuyabeno, Laguna Grande and surroundings, including Río Cuyabeno from Puerto Bolívar to above Laguna Canangueno, 00°00'S, 76°10'W, 265 m, 11 Mar 1990 (fl), *H. Balslev, C.C. Berg, M. Gavilanes, A. Thygesen, D.E. Christensen, L. Ellemann & R. Brucculeri 97496* (holotype: AAU; isotypes: ASU, F, QCA, SEL).

Frutex vel arbor, indumento flavescenti vel cano-flavescenti; ramulis teretis; foliis lanceolatis, chartaceis, 5.6–14 × 1.6–3 cm, longi acuminatis, basi obtusis; paniculis axibus gracilibus; baccis ellipsoideis.

Shrub or tree 2–10 m tall, the trichomes simple, yellowish to yellowish-white; branchlets terete, densely pubescent when young, peeling in thin strips when slightly older. **Leaf blades** lanceolate, 5.6–14 × 1.6–3 cm, membranous to chartaceous, the upper surface glabrous except for the midvein, drying olive-green to brownish, the lower surface paler, sparsely appressed-pubescent, the trichomes present especially along the venation; apex long-acuminate; base obtuse; midvein impressed above, pubescent, convex below; lateral veins 20–30 pairs, impressed above, sharply convex below; marginal vein 1, to ca. 1 mm from blade margin, indistinct above, slightly salient below; glands numerous, indistinct or minutely punctiform on both surfaces; petiole 1–3 mm long, channeled, densely pubescent. **Inflorescences** paniculate, axillary or mostly subterminal, with to ca. 20 flowers, 3–6.5 cm long, the axes appressed-pubescent, filiform; bracts and bracteoles early deciduous, not seen. **Flowers** 5-merous; buds obovoid to subglobose, 2–3 mm long; calyx-lobes triangular, to 1 mm long, appressed-pubescent without, glabrous within; petals suborbicular, ca. 2 mm diam., sericeous without; stamens numerous, the filaments ca. 3–4 mm long, the anthers ca. 0.3 mm long; style ca. 4 mm long, the stigma punctiform; hypanthium not prolonged beyond the ovary, sericeous without; disk ca. 2 mm diam., densely pubescent; ovary 2-locular; ovules 2 per locule. **Fruits** (immature) berries, ellipsoid, ca. 10 × 8 mm, crowned by the persistent calyx lobes, yellow, gland-dotted, puberulous

FIG. 4. *Myrcia aequatoriensis* M.L. Kawasaki & B.K. Holst (*Balslev et al. 97496*: Holotype, AAU; inset from isotype at SEL).

to glabrous; seed 1, ca. 8 × 7 mm, the seed coat membranous; embryo myrcioid, the cotyledons leafy and folded, the radicle elongate, equaling the cotyledons in length.

Distribution.—This species is known from a few collections from Sucumbíos (Reserva Faunística Cuyabeno) in northeastern Ecuador, and one collection from Imbabura in northwestern Ecuador; it occurs in lowland tropical rainforests at 220–500 m elevation.

Myrcia aequatoriensis belongs to sect. *Myrcia*, among the group of species related to the *M. fallax* (Rich.) DC. – *M. splendens* (Sw.) DC. complex. These species are separated by characters of the indumentum, leaf morphology, including venation and glands, inflorescences, and size of flower buds (McVaugh 1969). From this group, *M. aequatoriensis* is distinguished by the combination of these characters: lanceolate, thin, subsessile leaves, long-acuminate at the apex, obtuse at the base, with impressed lateral veins on the upper surface, and by delicate panicles with filiform axes.

Additional collections examined: **ECUADOR. Imbabura:** Lita, 501 m, 28 Apr 1949 (fr), *M. Acosta Solís 12296* (F). **Sucumbíos:** Reserva Faunística Cuyabeno, Laguna Grande and surroundings, including Río Cuyabeno from Puerto Bolívar to above Laguna Canangueno, 00°00'S, 76°10'W, 265 m, 11 Mar 1990 (fl), *H. Balslev et al. 97071* (AAU, QCA). Reserva Faunística Cuyabeno, Laguna Grande and surroundings, including Río Cuyabeno from Puerto Bolívar to above Laguna Canangueno, 00°00'S, 76°10'W, 265 m, 11 Mar 1990 (fl), *H. Balslev et al. 97217* (AAU, ASU, F, QCA, SEL). Estación Científica Cuyabeno, 220 m, 21 Jul 1992 (fr), *J. Jaramillo 14913* (NY, QCA). Reserva Faunística Cuyabeno, 1 ha plot ca. 1 km N of Laguna Grande and surroundings, 00°00'S, 76°12'W, 265 m, 11 Apr–10 Jun 1988 (st), *A.D. Poulsen 78348* (AAU-2 sheets, QCA).

Myrcia verticillata M.L. Kawasaki & B.K. Holst, sp. nov. (**Fig. 5**). Type: ECUADOR. Orellana (Napo on label): Estación Científica Yasuní, Río Tiputini, NW of confluence with Río Tivacuno, 6 km E of Maxus road, Km 44, detour to Tivacuno well, parcela 50 ha, 00°38"S, 76°30'W, 200–300 m, 21 Mar 1996 (fr), *K. Romoleroux & R. Foster 2147* (holotype: QCA; isotypes: F-2 sheets, SEL).

Frutex vel arbor, indumento brunneo vel flavo-brunneo; ramulis quadrangulatis; foliis verticillatis, oblanceolatis, coriaceis, 19–29 × 4–7.5 cm, abrupte acuminatis, siccatis atrobrunneis; paniculis 5–13 cm longis; baccis globosis, atropurpureis ubi matureis.

Shrub or tree 4–25 m tall, to ca. 20 cm dbh, the trichomes simple, brown to yellowish-brown; bark reddish, the stems quadrangular in cross section with rounded angles, densely pubescent. **Leaves** subsessile to short-petiolate, verticillate in 4-merous whorls; blades oblanceolate, 19–29 × 4–7.5 cm, coriaceous, the upper surface drying dark brown to brownish, puberulous, the lower surface paler, sparsely hirsute-pubescent, the trichomes present especially on the venation; apex abruptly acuminate; base obtuse; midvein hirsute, impressed above, convex below; lateral veins 15–20 pairs, these and major interconnecting tertiary veins impressed above, convex below; marginal veins 2, the innermost 2–4 mm from blade margin, similar in prominence to the lateral veins, the outermost less than 1 mm from margin; glands numerous, punctiform, indistinct above, evident below; petiole 3–9 mm long, stout, channeled, densely pubescent. **Inflorescences** paniculate, axillary, 5–13 cm long, the axes hirsutulous; bracts and bracteoles early deciduous, not seen. **Flowers** 5-merous; buds not seen; calyx-lobes ca. 1 × 2 mm, truncate to broadly rounded at apex, appressed-pubescent to puberulous without, glabrous within; petals, stamens, and style not seen; hypanthium not prolonged beyond the ovary; disk ca. 2 mm diam., hirsutulous. **Fruits** berries, globose, 1–1.7 cm diam., turning from green to yellow-orange to red, and finally purple-black (*Acevedo-Rdgz. & Cedeño 7628*), puberulous, crowned by the slightly overlapping calyx lobes; seeds 1 or 2, ca. 8–10 × 7–8 mm, the seed coat membranous; embryo myrcioid, the cotyledons leafy and folded, the radicle elongate, equaling the cotyledons in length.

Distribution.—This species is known only from northeastern Ecuador in Orellana province, in the region of Yasuní National Park; it occurs in primary, lowland wet forests, at 200–300 m elevation.

From all the other species of *Myrcia* in Ecuador (Holst 1999; Holst & Kawasaki 2008), *M. verticillata* is promptly recognized, even in sterile condition, by the large, oblanceolate, dark brown leaves (when dry), that are subsessile and verticillate, in tetramerous whorls, and by the quadrangular stems. Species of *Myrcia* with both opposite and verticillate leaves were described by Berg (1857) in Martius' Flora Brasiliensis, but at least in northern South America, *M. verticillata* is the only known species with leaves consistently in tetramerous whorls. *Myrcia verticillata* may be allied with the *Gomidesia* group of *Myrcia*; flowers are needed to confirm the relationship.

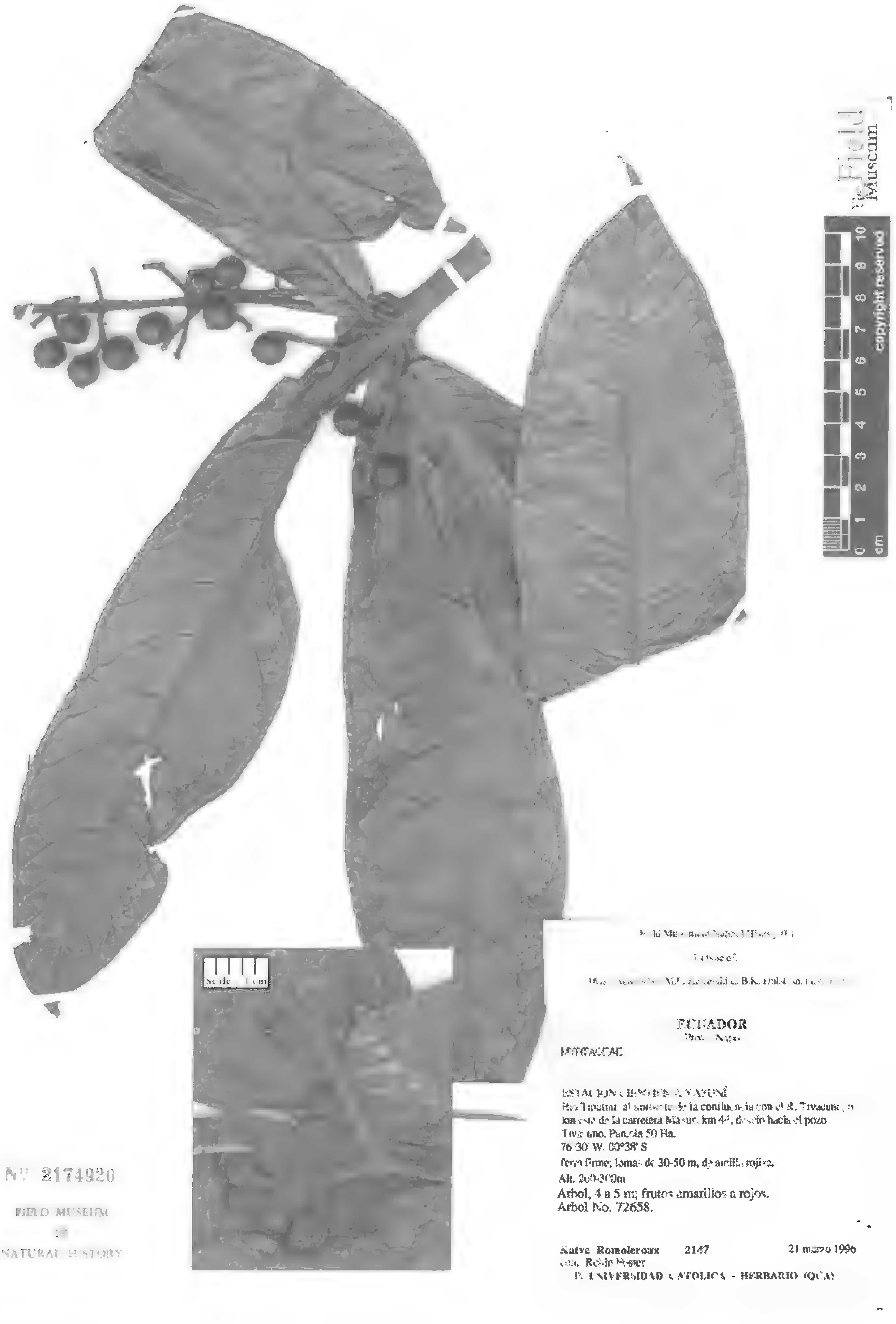

FIG. 5. *Myrcia verticillata* M.L. Kawasaki & B.K. Holst (*Romoleroux & Foster 2147*: Isotype, F; inset from *Neil et al. 8233*, SEL).

Additional collections examined: **ECUADOR. Orellana:** Yasuní Forest Reserve, along road between Km 70 and 100, E of PUCE Scientific Station, 0°50.014'S, 76°20.518'W – 0°54.730'S, 76°13.304'W, 200 m, 2 Jul 1995 (fr), *P. Acevedo-Rodríguez & J.A. Cedeño 7628* (SEL, US); Yasuní, Parque Nacional Yasuní, oil well Conoco-Amo 2, 00°57'S, 76°13'W, 230 m, 9–19 Jan 1988 (fr), *D. Neill et al. 8233* (F, MO, SEL); Aguarico, Yasuní, Reserva Etnica Huaorani, Maxus road and pipeline construction project, Kms 98–99, 00°55'S, 76°13'W, 250 m, 18 Jun 1994 (fr), *N. Pitman & G. Romero 299* (F, MO, QCNE, SEL); Estación Científica Yasuní, Río Tiputini, NW of confluence with Río Tivacuno, E of Repsol-YPF road, Km 7, detour to Tivacuno well, parcela 50 ha, column 29-02(2,3), 00°38'S, 76°30'W, 200–300 m, 17 Feb 2001 (fr), *G. Villa & L. Velez 912* (F, QCA).

ACKNOWLEDGMENTS

We are grateful to the curators and staff of the herbaria cited in the manuscript for providing the collections used in this study, especially to Henrik Balslev and Benjamin Øllgaard from AAU, and Ron Liesner and Jim Solomon from MO. Fred Barrie, Les Landrum, and Jim Luteyn offered helpful suggestions to improve this manuscript.

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FOLIA TAXONOMICA 12. *PARADRYMONIA* (GESNERIACEAE: EPISCIEAE) FROM THE GUIANA SHIELD: *P. MAGUIREI*, A NEW SPECIES FROM AMAZONAS, AND DISTRIBUTION AND FLORAL MORPHOLOGY OF *P. MACULATA*

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ABSTRACT

Paradrymonia maguirei is described from the state of Amazonas, Venezuela. The distribution of *Paradrymonia maculata* in Venezuela and the Guianas is documented, as well as its unusual corolla morphology.

RÉSUMÉ

Paradrymonia maguirei est décrit de l'état d'Amazonas, Venezuela. La répartition de *Paradrymonia maculata* au Venezuela et dans les Guyanes est documentée, ainsi que sa corolle de forme inhabituelle.

RESUMEN

Se describe **Paradrymonia maguirei** del estado de Amazonas, Venezuela. También se documenta la distribución de *Paradrymonia maculata* en Venezuela y las Guianas, así como su inusual morfología de la corola.

Hanstein (1854: 206) described the genus *Paradrymonia* Hanst. with only one species, *P. glabra* (Benth.) Hanst. (1854, p. 207, fig. 43), which is currently a synonym of *P. ciliosa* (Mart.) Wiehler. The name *Paradrymonia* was in use only for a short time as Hanstein (1864) reduced it to a synonym of *Episcia* Mart. When Wiehler (1973) re-established *Paradrymonia*, he transferred species from other genera. From *Drymonia* Mart. he took species that did not have the typical *Drymonia* anther dehiscence through a basal pore, and from *Episcia* Mart. he moved species that lacked stolons and did not otherwise belong to *Nautilocalyx* Linden ex Hanst. Currently *Paradrymonia* includes 38 species.

Recent molecular studies (Clark et al. 2006) have shown that it is likely that the species of *Paradrymonia* will separate into two natural groups of species, mostly with large leaves (20–50 cm long) and small axillary inflorescences, and a few isolated species. The larger group, true *Paradrymonia*, would mostly include species with petioles longer than the inflorescences and either with stems 5–10 mm thick and rooting at nodes on the substrate, and the smaller group has thinner and shorter stems and a "rosette-like" habit (Wiehler 1978). Those two groups are likely to stay in *Paradrymonia*. They are present in continental America from Mexico (Oaxaca) to Bolivia (Cochabamba) and eastward to Brazil (Amapá).

A few species in *Paradrymonia* have uncertain affinities. *P. anisophylla* Feuillet & L.E. Skog is an epiphyte with hanging stems and leaves strongly unequal in a pair; the molecular data (Clark et al. 2006) suggest that it may not be a *Paradrymonia*. The same data set places outside *Paradrymonia* an epiphyte with erect thick stems, *P. longifolia* (Poepp.) Wiehler. *Paradrymonia campostyla* (Leeuwenb.) Wiehler and *P. barbata* Feuillet & L.E. Skog from the Guianas are climbers with smaller leaves (3–15 cm long) and 1(–3) axillary flowers. Here two other hard-to-place species are dealt with: *P. maguirei*, a new species from Amazonas (Venezuela), which is vegetatively unlike other *Paradrymonia* species with a rosette-like habit, short petioles, and sharply biserrate paper-thin leaves, when dry; and *P. maculata* (Hook. f.) Wiehler with large condensed inflorescences and large bracts (see below) that is endemic to the Guiana Shield.

J. Bot. Res. Inst. Texas 3(1): 133 –138. 2009

A.—*Paradrymonia maguirei* Feuillet, sp. nov.

Although it seems obvious that the genus *Paradrymonia* will prove to be polyphyletic (Clark et al. 2006), in the absence of a comprehensive molecular study of *Paradrymonia*, along with *Nautilocalyx* and *Chrysothemis* Decne., the only reasonable option at the moment is to place this new species in *Paradrymonia* as *P. maguirei*. It does not belong in any of the other genera of the Episcieae (Weber 2004; Skog & Boggan 2006) and anticipating the split of *Paradrymonia* by describing a new genus without the proper data would be taking a high risk of creating a generic synonym.

Paradrymonia maguirei Feuillet, sp. nov. (**Fig. 1**). Type: VENEZUELA. Amazonas. Depto. Alto Orinoco: Cerro Marahuaca, slope forest, 1000 m, 3 May 1949, *B. Maguire & B. Maguire, Jr. 29185* (holotype: NY, pro parte: specimen A and material in the pocket).

= [*P. marahuacana* Wiehler] invalid: in sched.

Paradrymonia maguirei ab aliis speciebus a characteribus sequentibus differt. Planta pro parte majore, praeter infra foliis intervenia, indumento dense vestita, petiolo 2–2.5 cm longo, lamina foliorum supra velutina vel appressa pubescens, 10–11 × 7–8 cm, basi asymmetrica, apice obtuso rotundo, margine bi-serrata, in sicco membranacea.

Epiphyte or saxicolous. Stem creeping, 0.5 cm thick or more, 5 cm long (in the type collection), with a dense brown-red indumentum, apical few internodes with leaves, about 3 mm long, forming some kind of a loose pauci-leaved rosette. Leaves opposite, strongly unequal in a pair, the smaller about 2 cm long including petiole, ligulate, 2–3 mm wide; the larger with petiole 2–2.5 cm long, thick, covered with dense, long, brown-red trichomes; blade membranous when dry, elliptic, 10–11 × 7–8 cm, asymmetrically acute to obtuse at base, widely rounded at apex, margin sharply biserrate, above velutinous or appressed-pubescent, beneath appressed-pubescent or hirsute on veins. Inflorescence axillary, fasciculate; pedicels up to 2 cm long, with a dense, long, brown-red indumentum. Flowers with sepals lanceolate, long acuminate, 0.8–1.3 × 0.2 cm, with a dense, long, brown-red indumentum; corolla oblique in the calyx, with red trichomes outside, basal gibbosity 1–1.5 × 2 mm, tube cylindric, 1.8–2 cm long, lobes suborbicular, 0.8 × 0.6 mm, undulate at margin. Fruit not seen.

Distribution.—*Paradrymonia maguirei* is known only from the type collection from the area North of La Esmeralda in the Duida-Marahuaca National Park, on a forested slope of the Cerro Marahuaca (Amazonas, Venezuela), 65°24'W 3°40'N according to maps, at 1000 m elevation. It was blooming in May.

The color of the corolla is not known. There are two specimens that I marked A and B on the herbarium sheet in the New York herbarium. Specimen A, including the fragments in the pocket, is the type of the new species; it is on the middle left of the sheet and the pocket on the lower right above the label. Specimen B (sterile), on the upper right, is probably *Nautilocalyx cordatus* (Gleason) L.E. Skog. The only open corolla, preserved in the pocket, is very unlike the corolla of *N. cordatus* and is the one described here. The affinities of *Paradrymonia maguirei* in the genus are not clear. This species shows a unique combination of characters: rosette-like habit, petioles short, with dense, long, appressed pubescence, leaf blade drying paper-thin, asymmetric at the base, broadly rounded at the apex, and sharply biserrate at the margin. Other species with short petioles have leaf blades long-decurrent or are long stemmed epiphytic climbers. This species was *Paradrymonia* "sp. E" in the text and the key (Feuillet & Steyermark 1999).

Etymology.—The epithet *maguirei* refers to the senior collector, a great botanist, collector, and student of the flora of the Guiana Shield.

B.—Subgenus *Pagothyra*

Like other infrageneric taxa, *Episcia* sect. *Pagothyra* Leeuwenb. coined for *E. maculata* Hook. f. (Leeuwenberg 1958: 312) was never transferred to *Paradrymonia*, although *P. maculata* stands alone there as well as in *Episcia*.

Paradrymonia subg. **Pagothyra** (Leeuwenb.) Feuillet, comb. et stat. nov. Basionym: *Episcia* sect. *Pagothyra* Leeuwenb., Blumea 7:312. 1958.

Fig. 1. ***Paradrymonia maguirei*, photograph by C. Feuillet of the holotype *B. Maguire & B. Maguire, Jr. 29185* (NY).**

Paradrymonia maculata (Hook. f.) Wiehler, Selbyana 5:57. 1978. *Episcia maculata* Hook. f., Bot. Mag. 116: pl. 7131. 1890. [*Nautilocalyx maculatus*] Wiehler 1970, invalid: in sched. Type: CULTIVATED. Origin GUYANA: Cult. Hort. Kew., 2 Sep 1889 (*fl*), *collector unknown s.n.* (holotype: K; isotype: K; photographs of holotype BH, NY, U, US, WAG).

Paradrymonia maculata climbs by way of short roots at the nodes and along internodes, similar to *Hedera helix* L. The stems are tightly applied to the bark and have been reported to grow 1–3 meters high. The leaves are opposite and equal or subequal in a pair with a long petiole; the blade is large and broadly elliptic, with serrate margins. The pedunculate inflorescences are axillary, unilateral cymes, with bracts that are large, greenish yellow with purplish or reddish veins. The corolla is creamy yellow with reddish dots and the ventral lobe acts as a cover closing the tube. Longer descriptions can be found in Leeuwenberg (1958) and Skog & Feuillet (2008).

Distribution.—*Paradrymonia maculata* is known from the forests of French Guiana, Guyana, and Venezuela (Delta Amacuro) at 0–500 m. It has been collected in bloom every month of the year and in fruit in March, June, August, and December.

Corolla.—As noted and illustrated in Hooker (1890), the ventral lobe of the corolla of *Paradrymonia maculata* closes the tube (Fig. 2). The nectary gland is in dorsal position at the base of the ovary, next to the basal gibbosity forming a nectar chamber at the base of the 2.7–3.5 cm long corolla tube. The ventral corolla lobe is effectively a barrier between the nectar produced at the base of the tube and most pollinators. Exerting pressure on both sides on the apical third of the tube flips the ventral lobe from its position of convex lid closing the throat to a more classic concave corolla lobe by moving it more than 90°. It allows access to the nectar to strong pollinators, possibly carpenter bees. The bracts and sepals are pale yellow with red or purple veins. In the Guianas similar corolla morphology is found in a Solanaceae, *Markea formicarum* Dammer, where the lower lobe closes the throat. That species is lacking bracts, but the large calyx is cream- or straw-colored with purple veins, showing a similar color pattern as the bracts and calyces of *P. maculata*. It might be of interest to note that an Asian Gesneriaceae, *Agalmyla chorisepala* (C.B. Clarke) Hilliard & B.L. Burtt, has orange corollas with the ventral lobe closing the tube, but in this example the lobe flips at anthesis and opens the access to the tube without further obstacle to pollination.

The type of *Paradrymonia maculata* (Hook. f.) Wiehler from an unknown collector, comes from a plant cultivated at the Royal Botanic Gardens, Kew. It was blooming in September 1889. The plant was grown from material collected in British Guiana, now Guyana. Subsequent collections all came from Guyana and this limited distribution was acknowledged by Leeuwenberg (1958) and Wiehler (1978). During the completion of the treatment of the Gesneriaceae for *Flora of the Guianas* (Skog & Feuillet 2008), collections of *P. maculata* from Venezuela and French Guiana came to my attention. That species was not mentioned in the treatment for *Flora of the Venezuelan Guayana* (Feuillet & Steyermark 1999) but is present in the Antonio Díaz Department, the part of the state of Delta Amacuro neighboring Guyana. No collections from Surinam have been made, but it is likely that it is, or has been, present there.

Material studied: **VENEZUELA. Delta Amacuro. Depto. Antonio Díaz:** low forest, 12 km S of San José de Amacuro, 8°28'N 60°27'W, sea level, Feb 1987 (*fl*), *A. Fernandez 3903* (MO, MYF, NY, PORT, US); primary rain forest, Río Grande, 60 km NE of El Palmar, about 8°25'N 61°45'W, 120 m, 15 Mar 1987 (*fl*), *G. Aymard 5411* (PORT).

GUYANA. Arawai Creek, right bank of Essequibo Riv., Feb 1952 (*fl*), *C.A. Persaud 140 = F.D. (Forestry Department) 6897* (K, NY, U); Essequibo River, Kamuni Creek, Groete Creek, 14 Apr 1944 (*fl*), *B. Maguire & D.B. Fanshawe 22826* (F, GH, K, NY, U, US); Morawhanna, Oct 1905 (*fl*), *A.W. Bartlett 8600* (K); Rockstone, 15 July – 1 Aug 1921 (*fl*), *H.A. Gleason 664* (NY); Unabaruka Creek, Aug 1930 (*fl*), *E.B. Martyn 225* (BRG). **Barima. Waini:** Barima Riv., 15 mi E of Arakaka, 7°37'N 59°54'W, 38 m, 26 July 1986 (*fl*), *J.J. Pipoly 8059* (BRG, CAY, NY, US); Barima Riv., May 1907 (*fl*), *R.D. Ward s.n.* (K); Baramita airstrip – Millionaire trail, 7°22'N 60°28'W, 91 m, 3 Apr 1991 (*fl*), *T.D. McDowell et al. 4182* (NY, US); Matthews Ridge, Barima Riv., 23 Jan 1955 (*fl*), *R.S. Cowan 39337* (NY, US); Portage between Aruau Riv. & Yarikita Riv., 8°00'N 59°55'W, 17 Jan 1920 (*fl*), *A.S. Hitchcock 17601* (GH, K, NY, S, US); Sebai Riv., ± 5 km SW of Sebai Village, 15–20 m, 7°49'N 59°57'W, 16 Dec 1991 (*fr*), *B. Hoffman et al. 615* (US); Upper Aruau Riv., Aruka Riv., Apr–May 1929 (*fl*), *E.B. Martyn 53* (K); Upper Kaituma R.; 3 km w of Port Kaituma, 7°42'N 59°54'W, 0–5 m, 8 Dec 1991 (*fl*), *B. Hoffman & H. Benjamin 525* (US); Waini Riv., July 1906 (*fr*), *J.E. Beckett s.n.* (K, U). **Cuyuni. Mazaruni:** Aurora, helicopter landing, 6°47'N 59°44'W, 4 Oct 1989 (*fl*), *L.J. Gillespie 2084* (US; Bartica, 12–15 mi from town, 28 Aug 1935 (*fr*), *D. Potter 5358* (GH); Essequibo county, near Mazaruni Forest Station, 9 Aug 1934 (*fl*), *W.A. Archer 2432* (BRG, K, US); id., July–Sep 1942 (*fl*), *D.B. Fanshawe 785 = F.D. 3521* (K). **Essequibo Islands. West Demerara:** Macouria Riv., right bank of Lower Essequibo Riv., Nov 1886, *G.S. Jenman 2419* (K); Upper White Creek, near Blue Mountain, 6°35'N

Fig. 2. ***Paradrymonia maculata*****, photograph by Chris Davidson (Idaho Botanical Research Foundation).**

58°43'W, 5–20 m, 14 Apr 1993 (*fl*), *T.W. Henkel et al. 1879* (NY, US). **Pomeroon. Supenaam:** Pomeroon District, Mt. Russell, Mar 1886 (*fl*), *G.S. Jenman 2097* (K); Pomeroon Riv., 20 Aug 1959 (*fl*), *V. Graham 352* (K); Pomeroon Riv., Yawiami Creek, Aug 1882 (*fl*), *G.S. Jenman 1939* (K); Pomeroon Riv., Pomeroon District, 17–24 Dec 1922 (*fl*), *J.S. de la Cruz 3124* (F, GH, MO, NY, PH, UC, US); id., 14–20 Jan 1923 (*fl&fr*), *J.S. de la Cruz 3022* (GH, NY, PH, US); id., Mar 1884 (*fl*), *G.S. Jenman 2002* (K, NY); Abrahms Creek, Mar 1904 (*st*), *"G.S. Jenman" 7808* (BRG); 3 km SW of Kabakaburi Mission village, 7°15'N 58°45'W, 0–10, 25 Sep 1992 (*fl bud*), *B. Hoffman & L. Roberts 2839* (NY, US). **Potaro. Siparuni:** Garraway stream, 102,5 mi on Bartica – Potaro rd., 5°22'25"N 59°7'20"W, 38 m, 12 Mar 2004 (*fl*), *K.M. Redden 2231* (US); Iwokrama Rainforest Reserve, Karupukari – Annai Road, 4°28'14"N 58°47'16"W, 400–500 m, 21 Mar 1997 (*fl*), *H.D. Clarke, S.A. Mori & S. Heald 4181* (US); Kaieteur Falls, 5°10'N 59°29'W, 23 Oct – 3 Nov 1923 (*fl*), *J.S. de la Cruz 4395* (F, GH, NY, PH, US, VEN); Potaro, 10 mi S of Potaro landing, 5°10'N 59°00'W, 7–8 Jan 1920 (*fl*), *A.S. Hitchcock 17397* (GH, K, NY, S, US); North Fork Riv., 0.5–1.5 km N of Konawark Riv., 5°9'N 59°8'W, 137 m, 18 May 1991 (*fl*), *T.D. McDowell, C.L. Kelloff & A. Stobey 4819* (US). **Upper Demerara. Berbice:** Haiowa Falls, Essequibo Riv. basin, 5°7'N 58°49'W, 27 Sep 1937 (*fl*), *A.C. Smith 2123* (F, G, GH, K, NY, S, U, US); Mabura region, W Pibiri compartment, 5°01'95"N 58°37'73"W, 12 Oct 1993 (*fl*), R.C. *Ek, P.J.M. Maas, H. Mass & C. Görts 942* (U, US); Mabura region, Ekuk compartment, Holder Falls, 5°20'N 58°10'W, 21 Aug 1993 (*fl*), *R.C. Ek, R. Zagt, L. Brouwer & N. Eernisse 896* (US). **Upper Takutu. Upper Essequibo:** Maparri R., S bank, 3°20'N 59°15'W, 3 June 1996 (*st*), *H.D. Clarke & T. McPherson 1928* (US); Upper Rupununi Riv., near Dadanawa, 2°45'N 59°31'W, 13 June 1922 (*fl&fr*), *J.S. de la Cruz 1518* (CM, F, MO, NY, PH, US); id., 13 June 1922 (*fl*), *J.S. de la Cruz 1535* (CM, GH, F, MO, NY, PH, UC, US).

FRENCH GUIANA. Approuague Riv. Basin: Crique Cascade, 390 m, 15 Mar 2002 (*fl&fr*), *J.F. Smith, E. Teppe & C. Davidson 4134* (CAY). **Matoury:** Plateau de Nancibo, 4°40'N 520°30'W, 24 Oct 1983 (*fl*), *F. Billiet & B. Jadin 1857* (BR, CAY). **Oyapock Riv. Basin:** Crique Gabaret, 3°55'42"N 51°48'7"W, 15 Apr 1988 (*fl*), *G. Cremers 9951* (CAY, NY, P, U, US); Roche Touatou, 130 m, 20 May 1995 (*fl*), *J.-J. de Granville & G. Cremers 13009* (CAY).

ACKNOWLEDGMENTS

I thank Alain Chautems and an anonymous reviewer for their careful reading of the manuscript. I am grateful to Eduardo Garcia-Milagros who translated the abstract into Spanish. This work could not have been completed without the help of the curators of the herbaria CAY, K, MO, NY, P, and VEN who made available to me the material in their care. This is number 144 in the Smithsonian's Biological Diversity of the Guiana Shield Program publication series.

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NEW SPECIES OF *BACCHARIS* (ASTERACEAE: ASTEREAE) FROM RIO DE JANEIRO STATE, SOUTHEASTERN BRAZIL

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ABSTRACT

Two new species of *Baccharis* from the state of Rio de Janeiro, southeastern Brazil, are described and illustrated. **Baccharis altimontana** Heiden, Baumgratz & Esteves, assigned to sect. *Caulopterae* DC., is characterized by the erect-patent branches, female capitulum with urceolate or campanulate involucre and uniseriate female pappus. The species is contrasted with morphologically close species of the "*Baccharis genistelloides* Complex." **Baccharis friburgensis**, assigned to sect. *Oblongifoliae* DC., is characterized by the coriaceous leaves with acute to obtuse apex, entire and revolute margin, corymbiform panicles, few-flowered male and female capitula and female florets with denticulate corolla apex, and those characteristics differentiate it from *B. macrophylla* Dusén. Additionally, keys to identify the species of sect. *Caulopterae* and sect. *Oblongifoliae* occurring in the state of Rio de Janeiro are provided.

RESUMO

Duas novas espécies de *Baccharis* do estado do Rio de Janeiro, sudeste do Brasil, são descritas e ilustradas. **Baccharis altimontana** Heiden, Baumgratz & Esteves, pertencente à sect. *Caulopterae* DC., é caracterizada pelos ramos ereto-patentes, capítulo feminino com invólucro urceolado ou campanulado e papilho das flores femininas unisseriado, a espécie é comparada com outras morfologicamente próximas do "Complexo *Baccharis genistelloides*." **Baccharis friburgensis** Heiden, Baumgratz & Esteves, pertencente à sect. *Oblongifoliae* DC., é caracterizada pelas folhas coriáceas, com ápice agudo ou obtuso, margem inteira e revoluta, panículas corimbiformes, capítulos masculinos e femininos paucifloros e flores femininas com ápice da corola denticulado, características que a diferenciam de *B. macrophylla* Dusén, espécie morfologicamente similar. Adicionalmente, são fornecidas chaves para determinação das espécies das seções *Caulopterae* e *Oblongifoliae* ocorrentes no estado do Rio de Janeiro.

INTRODUCTION

Baccharis was never revised taxonomically as a whole. The last worldwide compilation of accepted scientific names and synonyms of the genus was published by Malagarriga (1977). Following Müller (2006), infrageneric classification of *Baccharis* is still not well resolved, and, additionally due to the high species number, revisionary work in the genus is only possible with a geographical approach. For Brazil, the last revisionary work of the genus was provided by Barroso (1976), comprising 125 species. Later, Oliveira et al. (2006) published a compilation of 146 names, without citing vouchers to assure some occurrences of species not listed by Barroso (1976) in the country. The genus occurs in all Brazilian biomes and most of its species are concentrated in the central and eastern regions of the country, growing mainly in savannas (*cerrado*) and grasslands (*campos de altitude*, *campos rupestres* and *campos sulinos*). For the state of Rio de Janeiro information concerning the genus is available only in geographically restricted florulas (Barroso 1957, 1959; Esteves & Barroso 1996) or in the taxonomic revision for Brazil (Barroso 1976).

During the taxonomic revision of *Baccharis* for the flora of the state of Rio de Janeiro two new species belonging to the sect. *Caulopterae* DC. and sect. *Oblongifoliae* DC. were recognized. These new species are described and illustrated, and keys to identify the species of these sections occurring in Rio de Janeiro state are presented.

MATERIAL AND METHODS

The study has been based on literature revision and the examination of material or photos from herbaria GUA, HAS, HB, HBR, HPNI, HRJ, M, P, R, RB, RBR, RFFP, RUSU and SP. Specimens of the related taxa contrasted to the new taxa are cited just after the description and before the keys. The terminology used in the morphological descriptions is based on Radford et al. (1974) and Müller (2006). The measures were taken by the mean of a digital calliper in the wider portion of the structures. All colours mentioned are of dried mature structures. The illustrations were prepared by stereomicroscopy using a Carl Zeiss Stemi SV6. The conservation status is presented following the IUCN (2001) guidelines.

TAXONOMY

Baccharis altimontana Heiden, Baumgratz & Esteves, sp. nov. (**Fig. 1**). Type: BRAZIL: Rio de Janeiro: Teresópolis, Serra dos Órgãos, 27 Nov 1933, ♀*Brade 12510* (holotype: R!).

Ad *Baccharis* sect. *Caulopterae* DC. pertinens, *B. genistelloides* (Lam.) Pers. subsp. *genistelloides* similis sed ramis erecti-patentibus (non erectis) munitis, corolla florum masculinorum 2.9–4 mm longis (non 4–6 mm longis), corolla florum foemineorum 2.5–3.4 mm longis (non 3.5–6.8 mm longis), et pappi florum foemineorum uniseriati (non multiseriati) munito differt.

Dioecious subshrubs 0.2–0.4 m tall, erect-patent or prostrate. **Stems** and branches 3-winged, wings 0.5–6.5 cm long, 0.3–1.6 cm wide, plane to undulate, strongly resinous, seemingly glabrous, indument tufted, tufts appearing under magnification as small resinous dots. **Leaves** 0.3–2 mm long, 0.2–0.5 mm wide, bract-like. **Panicles** 18–24 cm long, of pseudospikes 3–18 cm long, capitula solitary or 2–3, sparsely along the axis, the main pseudospike longer than the axillary ones. **Male capitula** 4–5.5 mm long, involucre 4.4–6.5 mm long, 4–6.8 mm wide, urceolate to campanulate; pyllaries in 5–8 series, abaxial surface pale yellow to dark, outer and median phyllaries ovate, inner elliptical, apex entire or denticulate, margins light yellow, denticulate, scarious; clinanthium obconical, plane, alveolate, densely covered by biseriate trichomes. **Male florets** 35–63; corolla 2.9–4 mm long, 5-laciniate, tube 1.8–2.5 mm long, throat 0.2–0.4 mm long, cup-shaped, lobes 1–1.4 mm long, externally with sparse biseriate trichomes on the throat and tube; styles 3.2–4 mm long., apex 1/2-bifidous; pappus 3.2–4.2 mm long, uniseriate, apex slightly broadened, terminal cell ends slightly protruding. **Female capitula** 6.5–8 mm long; involucre 4.4–6.5 mm long, 4–6.8 mm wide, urceolate to campanulate; phyllaries in 6–9 series, abaxial surface pale yellow to dark brown or olive green, outer ovate, median ovate to elliptical, internal elliptical, apex entire or denticulate, margins light yellow, denticulate, scarious; clinanthium obconical, alveolate, densely covered by biseriate glandular trichomes, paleae absent. **Female florets** 34–42; corolla 2.5–3.4 mm long, filiform, apex shortly ligulate, 3–5 teeth of unequal size; styles 3.1–5.1 mm long, branches 0.5–0.8 mm long. **Cypselae** 1.2–1.5 mm long, cylindrical, glabrous, papillose, 16–22-ribbed; pappus 4–4.7 mm long, uniseriate, not-accrescent.

Specimens examined. **BRAZIL. Rio de Janeiro:** Itatiaia, 4 Nov 1965, *Eiten 6612* (RB); 12 Sep 2007, *Heiden & Baumgratz 823* (RB); 17 Dec 2007, *Heiden 932, 933* (RB); 13 Apr 2008, *Heiden 994* (RB); 18 Oct 1977, *Landrum 2103* (RB); 5 Dec 1964, *Vianna 207* (GUA, RB). **Nova Friburgo:** 22 Mar 2008, *Heiden & Baumgratz 711* (K, RB). **Teresópolis:** 27 Jun 2007, *Heiden 791, 792* (RB); 26 Sep 2007, *Heiden 879, 880* (RB); 21 Mar 2007, *Nadruz 1772* (RB); 6 Sep 1981, *Ribeiro 138* (GUA); Jan 1952, *Vidal II-173, II-175* (R); 12 Feb 1952, *Vidal II-551* (R) Feb 1952, *Vidal II-662* (R); 15–20 Dec 1952, *Vidal II-5768* (R); Feb 1953, *Vidal 1478* (R).

Distribution & ecology.—*Baccharis altimontana* is restricted to southeastern Brazil, known up to now only from the state of Rio de Janeiro. It occurs in the Atlantic Rain Forest biome, above 1900 m, in the massifs of Itatiaia (Serra da Mantiqueira), Serra dos Órgãos, Pico da Caledônia and Pico do Desengano (all of them belonging to the Serra do Mar). It grows in rather small populations in rock grooves on bare rock outcrops along the high altitude grasslands, preferably in places with constant wetness. Flowering and fruiting time is between September and December.

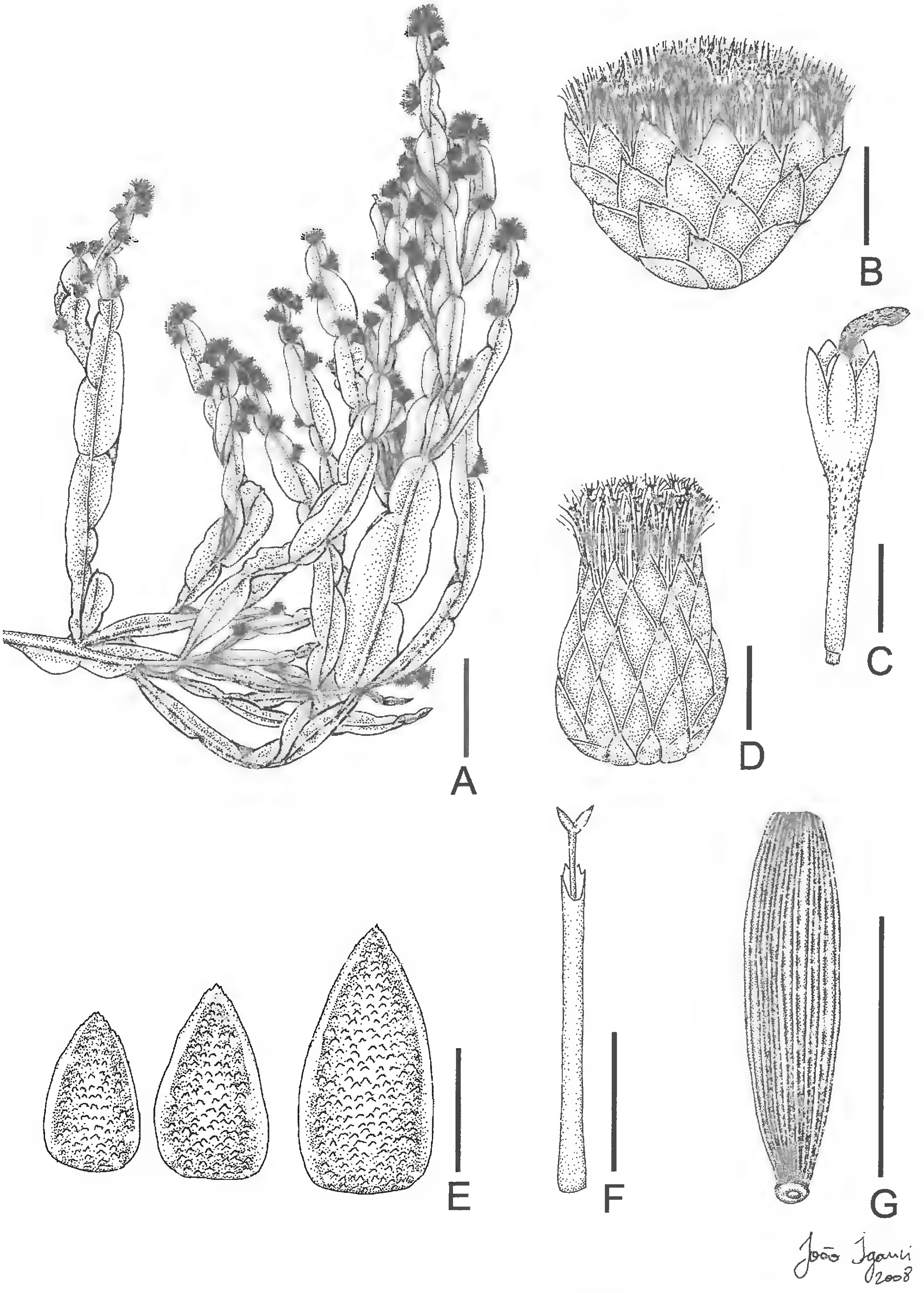

Fig. 1. *Baccharis altimontana* Heiden, Baumgratz & Esteves: A. Habit of female plant; B. Male capitulum; C. Male floret (pappus removed); D. Female capitulum; E. Phyllaries from female capitulum; F. Female corolla and style; G. Cypsela. Scale bar near A: 3 cm; B, D: 2 mm; C, E, F, G: 1 mm. (A: *Brade 12510*; B, C: *Heiden 879*; D, E, F, G *Heiden 823*). Drawn by João Iganci.

Vernacular.—Carqueja (Ribeiro 138; Heiden 711, 791, 792, 823, 879, 880, 932, 933, 994).

Conservation.—Common in high altitude grasslands, the species is considered near threatened (NT) due to the loss of quality of the mountainous environments caused by anthropogenic pressures.

Etymology.—The name refers to the habitat along the summits of mountain ranges.

Notes.—*Baccharis altimontana* is assigned to the sect. *Caulopterae* DC., mainly due to presence of winged stems, epaleaceous clinanthia densely covered with biseriate glandular hairs, papillose glabrous achenes, and pappus bristles of female flowers enlarged basally and fused into a ring. The species belongs to the "Baccharis genistelloides Complex" comprising at least eight morphologically close taxa [*B. crispa* Spreng., *B. genistelloides* (Lam.) Pers. subsp. *genistelloides*, *B. genistelloides* subsp. *lorentzii* Joch.Müll., *B. jocheniana* Heiden & Macias, *B. myriocephala* DC., *B. opuntioides* Mart. ex Baker and *B. riograndensis* Malag. & J. E. Vidal]. The new taxon is closer related to *Baccharis genistelloides* subsp. *genistelloides*, which occurs along the Andes from Colombia to northern Chile and Bolivia (Müller 2006). The studied specimens of *B. altimontana* were found in herbaria identified as *B. crispa*, *B. genistelloides*, *B. myriocephala*, *B. opuntioides* or *B. trimera* (= *B. crispa*).

Baccharis altimontana may be distinguished of *B. genistelloides* subsp. *genistelloides* by male corollas 2.9–4 mm long, female corollas 2.5–3.4 mm long and female florets with uniseriate pappus (vs. male corollas 4–6 mm long, female corollas 3.5–6.8 cm long and female florets with multiseriate pappus).

Specimens of *B. altimontana* are commonly identified as *B. opuntioides*, since Barroso (1976) merged both species in a broad circumscription of *B. opuntioides*. However, we consider *B. opuntioides* as endemic to the Serra do Caparaó at the boundary between the states of Espírito Santo and Minas Gerais. This species may be recognized by erect branches with short wings, 0.3–1.8 cm long and 0.2–0.8 cm wide, pseudospikes with apically crowded capitula (in the apical 1–2.5 cm), with the secondary branches longer than the main axis of the capitulescence, male corolla 4–5.2 mm long, female corolla 4.2–5 mm long and cypselae 0.8–1 mm long.

Baccharis altimontana may be distinguished from *B. crispa* by erectopatent or prostrate stems and shortly ligulate corollas of female florets with teeth of irregular size (vs. erect stems, corolla of female florets truncate or denticulate), and from *B. myriocephala* by the height (0.2–0.4 m tall), panicles 18–24 cm long with pseudospikes 3–18 cm long, involucre of female capitulum urceolate to campanulate (vs. height 100–250 cm, panicles 25–80 cm long, pseudospikes 10–35 cm long and involucre of female capitulum cylindrical).

Selected additional specimens:

Baccharis crispa Spreng., Syst. veg. 3:466. 1826. **BRAZIL. Rio de Janeiro:** Itatiaia, 13 Apr 2008, *Heiden 978, 993* (RB); Mar 1894, *Ule 177* (R); Resende, 12 Nov 2007, *Heiden & Baumgratz 815* (RB); 13 Sep 2007, *Heiden & Baumgratz 833, 834, 850, 851* (RB). **URUGUAY. Montevideo:** 1821/1822, *Sellow d397* (ISOTYPE: R).

Baccharis genistelloides (Lam.) Pers., Syn. pl. 2:425. 1807. **BOLIVIA. Santa Cruz:** 13 Nov 1959, *Maguire & Maguire 44496* (RB). **EQUADOR. Cotopaxi:** "province de Tacunga," *Jussieau s.n.* (P-Lam, photo of holotype). **Pichincha:** San Juan, 28 Nov 1952, *Fagerlind & Wibom 1556* (R).

Baccharis myriocephala DC., Prodr. 5:426. 1836. **BRAZIL. Minas Gerais:** *Vauthier 265* (G-DC, photo of lectotype). **Rio de Janeiro:** Miguel Pereira, 18 Apr 2007, *Heiden & Baumgratz 727* (RB). Resende, 26 Jul 1966, *Eiten 7447* (RB); 12 Nov 2007, *Heiden & Baumgratz 802, 803* (RB); Rio de Janeiro, Jun 2000, *Esteves & Esteves 462* (RB); Santa Maria Madalena, 14 May 2007, *Heiden 734, 735* (RB); Teresópolis, 27 Jun 2007, *Heiden 779, 780* (RB); 26 Oct 2007, *Heiden 878* (RB).

Baccharis opuntioides Mart. ex Baker *in* Martius, Eichler & Urban, Fl. bras. 6(3):39. 1836. **BRAZIL. Espírito Santo/Minas Gerais:** Caparaó, 15 Nov 1960, *Flaster 101* (GUA); Nov 1922, *Lobo s.n.* (R 37944); 8–12 Mar 1917, *Lutz 1197* (R); *Martius s.n.* (M, photo of holotype); 21 Oct 1947, *Moreira 44* (R); 11 Jul 1998, *Oliveira 1468* (GUA); 29 Jun 1950, *Santos s.n.* (R 52182); 2 Jul 1888, *Schwacke s.n.* (R 37949).

KEY TO *BACCHARIS* SECT. *CAULOPTERAE* IN RIO DE JANEIRO STATE, BRAZIL

1. Stems apterous.
   2. Leaf blades coriaceous, margins entire, with 3 acrodromous basal veins; panicles 1.5–6 cm long ____ **B. organensis**
   2. Leaf blades cartaceous, margins crenulate, pinnately veined or with 3 acrodromous 1–5 mm distant from leaf base suprabasal veins; panicles 4–16 cm long ____ **B. regnellii**
1. Stems winged.
   3. Leaves well-developed.
      4. Subshrubs (0.5–1 m tall); pseudospike branches 5–20 cm long ____ **B. junciformis**

4. Shrubs (0.5–3 m tall); pseudospike branches 0.5–5 cm long.
   5. Wings 1–3 mm wide; leaf blades coriaceous, with attenuate base ________ **B. burchellii**
   5. Wings 5–13 mm wide; leaf blades papiraceous, with cuneate or rounded base ________ **B. glaziovii**

3. Leaves bract-like.
   6. Branches erect; female corolla apex truncate or irregularly denticulate ________ **B. crispa**
   6. Branches erectopatent, scandent, decumbent and/or erect-prostrate; female corolla apex short ligulate.
      7. Subshrub 0.2–0.4 m tall; pseudospikes 3–18 cm long; capitula solitary or 2–3; involucre of female capitulum urceolate to campanulate ________ **B. altimontana**
      7. Subshrub 1–2.5 m tall; pseudospikes 10–35 cm long; capitula solitary or glomerules with 2–8 capitula; involucre of female capitulum cylindrical ________ **B. myriocephala**

Baccharis friburgensis Heiden, Baumgratz & Esteves, sp. nov. **(Fig. 2)**. Type: BRAZIL: Rio de Janeiro: Nova Friburgo, Macaé de Cima, 16 Aug 1989, ♂, *Vieira 48* (holotype: RB!; isotypes: FCAB!, GUA!, NY, R!, RB!, RBR!, SP!).

Ad *Baccharis* sect. *Oblongifoliae* DC. pertinens, *B. macrophyllae* Dusén habitu, foliorum coriaceo, inflorescentia in corymbis contracta similis, sed capitulis foemineis 2 ad 3 floribus (non 11 ad 21 floribus) munitis, corolla florum foemineorum apice dentato (non ligulato), et capitulo masculo 8 ad 12 floribus (non 30 ad 45 floribus) munito differt.

Dioecious shrubs 1.5–2 m tall. **Stems** erect, branching dichotomous, shoots glabrescent, with uniseriate and pedestal trichomes. **Leaves** spirally alternate, crowded at the apex of the branches, with petioles 0.2–0.8 cm long; blades 30–68 mm long, 7–21 mm wide, coriaceous, narrowly elliptic or oblanceolate to obovate, base attenuate, apex acute to obtuse, margins entire, revolute; pinnately veined; both surfaces seemingly glabrous, abaxial surface with tufted indument appearing as resinous dots, scarce biseriate, uniseriate and pedestal trichomes among the tufts. **Panicles** 1.9–4.4 cm long, 1.8–5.5 cm wide, corymbose, terminal; peduncles 1–1.8 cm long. **Male capitula** 2.9–4.8 mm long, involucre 2.9–4.8 mm long, cup-shaped, 2.7–5 mm wide; phyllaries in 3–5 series, brown, outer and median phyllaries ovate, inner linear-ovate, apex fimbriate, margins light-brown, shortly dentate; clinanthium convex, glabrous; paleae absent. **Male florets** 8–12, apex 5-laciniate; corolla 2.3–2.5 mm long., tube 0.9–1.1 mm long, externally densely covered by biseriate trichomes near the apex, throat 0.5–0.6 mm long, cup-shaped, lobes 0.7–0.8 mm long, apex not revolute; anthers included; styles 2.4–2.6 mm long, apex capitate by sweeping hairs of unequal size, slightly exserted; sterile ovary 0.5–0.7 mm long; pappus 2–2.3 mm long, uniseriate, apex broadened, cell ends erectopatent, shortly protruding. **Female capitula** 5.3–5.8 mm long, involucre 4.3–5 mm long, 2.2–3.1 mm wide, cylindrical; phyllaries in 4–6 series, brown, outer phyllaries ovate, median linear-ovate, inner linear, apex long-fimbriate, margins light-brown, shortly dentate; clinanthium convex, paleae linear, acute, deciduous. **Female florets** 2–3, filiform; corolla 2.9–3.2 mm long, apex 5-denticulate, distal half with subapical scattered biseriate trichomes; styles 3–3.5 mm long., branches 0.3–0.6 mm long. **Cypselae** 2–2.6 mm long, 0.4–0.6 mm wide, light brown, cylindric, narrowed at both extremities, with 5–6 longitudinal ribs, with scattered biseriate trichomes near the apex; pappus 2.5–3 mm long, slightly shorter to slightly longer than the style, biseriate, persistent, not accrescent at maturity.

Additional specimens examined. **BRAZIL. Rio de Janeiro:** Nova Friburgo, ♀, 24 Aug 1986, *Leitman 196* (K *n.v.*; RB-2x); ♂, 19 Aug 1990, *Moraes 414* (RB-2x).

Distribution & ecology.—Restricted to southeast Brazil (state of Rio de Janeiro). It occurs in the Atlantic Rain Forest biome, from 1000 to 1500 m above sea level, and is endemic to the summits of the Macaé de Cima Mountains, a part of the Organ Mountains/Serra do Mar Ranges. It grows directly on rock outcrops, along river headwaters or in edges of nebular forest. Flowering and fruiting in August.

Conservation.—Taking into account the few collections available, the restricted area of occurrence and the presence of anthropogenic pressure in surrounding areas, represented by cattle grazing, agriculture, tourism and urban expansion, the species is considered endangered (EN B2ab[iii]).

Etymology.—The name refers to the type locality in the municipality of Nova Friburgo.

Notes.—*Baccharis friburgensis* is assigned to sect. *Oblongifoliae* DC. for the pinnately veined leaves, capitate style apex in male flowers due to sweeping hairs of unequal size, paleate female capitula and female flowers with the pappus not elongated at cypsela maturity. The species is remarkable for the few-flowered

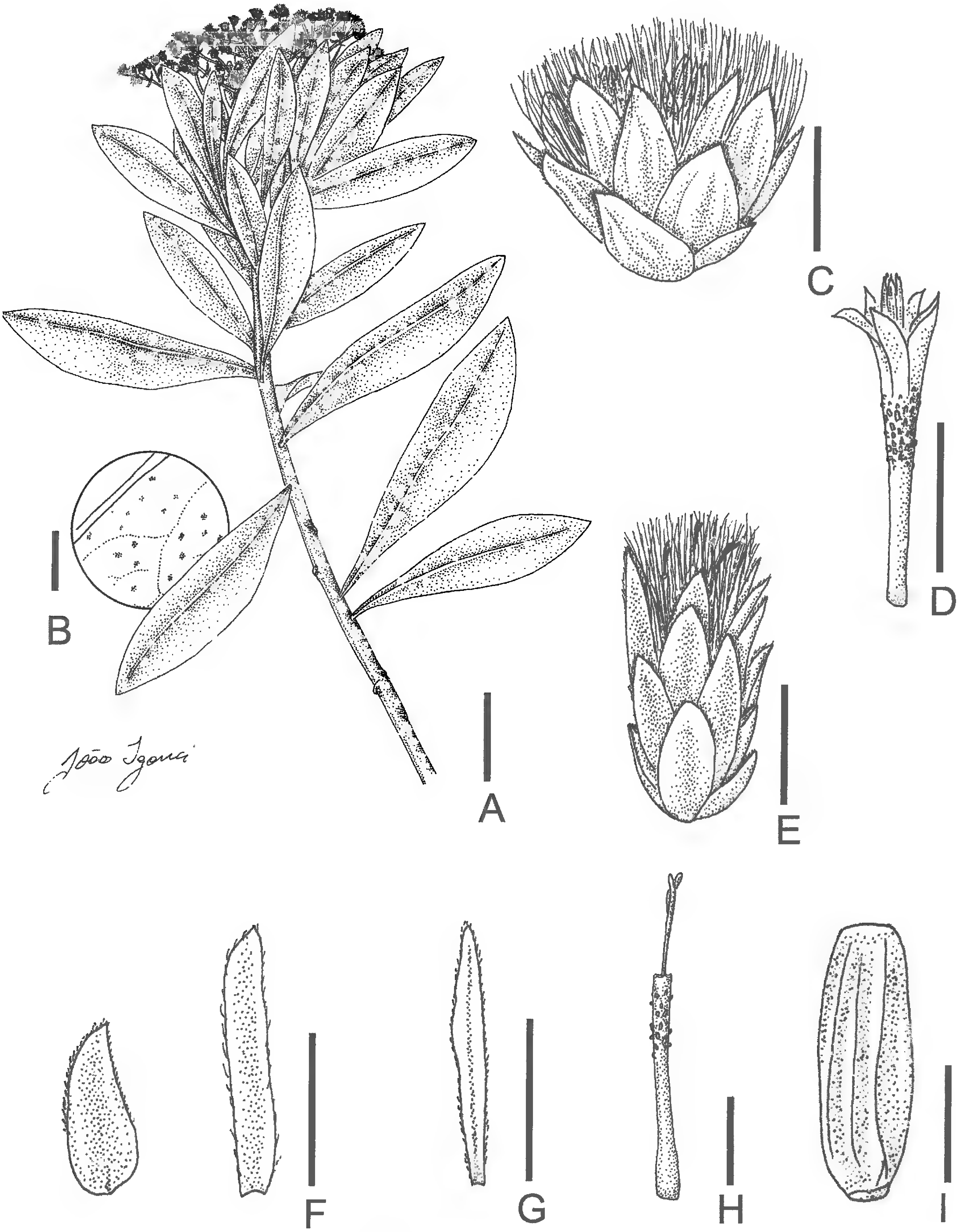

Fig. 2. *Baccharis friburgensis* Heiden, Baumgratz & Esteves: A. Branch of female plant; B. Abaxial leaf surface; C. Male capitulum; D. Male floret (pappus and sterile ovary removed); E. Female capitulum; F. Phyllaries from female capitulum; G. Palea; H. Female corolla and style; I. Cypsela. Scale bar near A: 2 cm; B, D, F, G, H, I: 1 mm; C, E: 2 mm (A, B, E, F, G, H, I: *Leitman 196*; C, D: *Vieira 48*). Drawn by João Iganci.

male (8–12) and female (2–3) capitula, which results in seemingly epaleaceous female clinanthia, because all paleae are, due to the low flower number, more distal then the distalmost flowers and hidden by the innermost phyllary series. Some further distinguishable characters are the coriaceous leaves with acute to obtuse apex, entire and revolute margins, and the corymbose panicles. *Baccharis* friburgensis is vegetative morphologically similar to the allopatric *B. macrophylla* Dusén, although this similarity seems to be a convergence to the habitat in sunny habitats on summits of mountains. The later one has leaf margin more commonly with 1–5 subapical teeth, seldom entire, male capitula with 30–45 flowers, female capitulum with 11–21 flowers, and female corollas ligulate.

Selected additional specimens:

Baccharis macrophylla Dusén, Arq. Mus. Nac. Rio de Janeiro 13:14. 1905. **BRAZIL. Rio de Janeiro:** Itatiaia, *Dusén 4844* (HOLOTYPE: R); 23 Jul 1960, *Handro 941* (SP); 17 Dec 2007, *Heiden 930* (RB); 16 Aug 1969, *Sucre 5775* (CEPEC); *s.d.*, *Tamandaré & Brade* 6562 (SP); Resende, 12 Sep 2007, *Heiden & Baumgratz 827, 828* (RB); Jul 1902, *Moreira & Teixeira s.n.* (R 38027).

KEY TO *BACCHARIS* SECT. *OBLONGIFOLIAE* IN RIO DE JANEIRO STATE, BRAZIL

1. Panicles pyramidate.
   2. Foliar indument ferruginous ____ **B. rufidula**
   2. Foliar indument not ferruginous ____ **B. oblongifolia**
1. Panicles corymbose.
   3. Leaf blade papyraceous, margins not revolute ____ **B. grandimucronata**
   3. Leaf blade coriaceous, margins revolute.
      4. Male capitula 30–45 florets; female capitula 11–21 florets, female corollas with ligulate apex ____ **B. macrophylla**
      4. Male capitula 8–20 florets; female capitula 3–8 florets, female corollas with denticulate apex ____ **B. friburgensis**

ACKNOWLEDGMENTS

The authors acknowledge the consulted herbaria, André Scarambone Zaú, Cecília Cronemberger de Faria, Denise Pinheiro da Costa, Izar Aximoff, Marcus Nadruz and Marina Wolowski Torres for providing field support, João Iganci for the illustrations, Jochen Müller for the valuable comments and an anonymous reviewer.

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BOOK REVIEW

Bruce M. Pavlik. 2008 **The California Deserts: An Ecological Rediscovery.** (ISBN 978-0-520-25145-8, pbk.). University of California Press, 2120 Berkeley Way, Berkeley, California 94704-1012, U.S.A. (**Orders:** The University of California Press c/o California/Princeton Fulfillment Services, 1445 Lower Ferry Road, Ewing, New Jersey 08618, U.S.A.; www.ucpress.edu, email orders@cpfsinc.com, 1-800-777-4726, 1-800-999-1958 fax). $27.50, 365 pp, numerous figures, graphs, images, maps, tables, references, index, and art credits, 7" × 10".

The California Deserts: An Ecological Rediscovery, is divided into seven sections that specifically describe the origins, discovery, climate, geology, resources, fauna, and flora that inhabit the 25 million acres that form the three deserts of California: the Sonoran, Mojave, and Great Basin Deserts. Author Bruce Pavlik threads stories of various early explorations throughout the first section of this book, providing the reader with descriptive information on how human inhabitants first found this desolate yet diverse ecosystem. Pavlik describes the extreme environment that is found within these deserts, how climate and species composition were the driving factors for shaping modern day deserts, and how most deserts are found between 10° and 30° latitude north and south of the equator. The three deserts are in fact very different, and these differences can be seen in their size, elevational range, precipitation, temperature, and communities that are present within each.

Pavlik describes the "remarkable biota" that can be found within the California desert region. A prime example is the kangaroo rat, an animal that has adapted to the harsh environment by its ability to procure water (a scarce resource) from seeds. He concludes the book by listing the current threats (e.g. fragmentation, invasive species) of this region and provides management ideas for restoring the deserts.

I found this book to be very informative and a wonderful resource for any naturalist, educator, or person that is eager to learn more about the diversity of the unique desert ecosystems of California. I believe the author enhanced this book by including a vast number of examples of the flora and fauna that are found within these regions. The images that were used throughout the book provided the reader with a vivid picture of this unique ecosystem. I would recommend this book to anyone that is interested in learning more about California deserts.—*Keri McNew, MS Biology, Programs Manager, Botanical Research Institute of Texas, 500 E 4th Street, Fort Worth, TX 76102, U.S.A*

DIPLYCOSIA INDICA (ERICACEAE): A NEW SPECIES AND A NEW GENERIC RECORD FOR INDIA

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ABSTRACT

Diplycosia Blume (Ericaceae)—a new generic record and **Diplycosia indica** M.R. Debta & H.J. Chowdhery—a new species from India is described and illustrated.

Key Words: *Diplycosia*, India, new species, new generic record

RESUMEN

Diplycosia Blume (Ericaceae)—nueva cita genérica, y se describe e ilustra **Diplycosia indica** M.R. Debta & H.J. Chowdhery—una nueva especie de la India.

INTRODUCTION

The genus *Diplycosia* consisting of about 99 species (Mabberley 1997), is widely distributed in the Malaysian region. Sleumer (1967) revised the genus for *Flora Malesiana* treating 97 species. He reported that the genus has its highest diversity in Borneo, while Mt. Kinabalu has the highest concentration of species. Powell and Kron (2001), based on molecular studies, have suggested treating *Diplycosia* under *Gaultheria* L. Argent (2002)—while studying *Diplycosia* from Borneo and peninsular Malaysia—described seven new species, one new form, and made two new combinations. *Diplycosia* can be distinguished from *Gaultheria* with the following key.

KEY TO THE GENERA *DIPLYCOSIA* AND *GAULTHERIA*

1. Flowers in fascicles; anther cells unawned, not aristate, with short or long apical tubules at apex; tubules connate or free ______ **Diplycosia**
1. Flowers in racemes; anther cells awned or aristate, not having apical tubules at apex ______ **Gaultheria**

During a 2006 plant collecting expedition to Singalila National Park (West Bengal), in the eastern Himalayan phytogeographic zone, some interesting and unusual plant specimens belonging to the family Ericaceae were collected. Initially they were identified as species of *Gaultheria*, but detailed studies revealed that some of the specimens belonged to the closely allied genus *Diplycosia*, which is hitherto unknown from India. Further critical examinations of the specimens have shown that though one specimen had some resemblance to a Malaysian species, *Diplycosia aperta* J.J. Sm., but differs widely from it in habit, leaf venations, number of flowers, bracteoles, and calyx character. The new collection is therefore described as a new species, *Diplycosia indica*, which is also a new generic record for India. Table 1 shows the differences with its allied species *Diplycosia aperta*. An illustration of the new species is provided for easy identification.

Diplycosia indica M.R. Debta & H.J. Chowdhery, sp. nov. (**Fig. 1**). Typus: INDIA. West Bengal: Darjeeling district, Singalila National Park, from Kainyakata to Kalapokhri, ca. 2950 m, 02 Jun 2006, *M.R. Debta* 40813 (holotypus: CAL; isotypus: BSD).

Species nova *Diplycosia aperta* J.J. Sm. arte affinis, sed habitu terrestri; inflorescentiis 4–6-floratis; floribus multum brevioribus, albis; pedicellis glabris; calycibus puberulis et bracteolis acutis ad acuminatis, sparse puberulis differt.

Terrestrial, prostrate shrubs, up to 1.5 m high. Stems terete, laxly to densely brown-hirsute or setose, reddish. Leaves subcoriaceous, 13–36 mm long × 7–18 mm wide, elliptic to ovate-elliptic, mucronate or apiculate,

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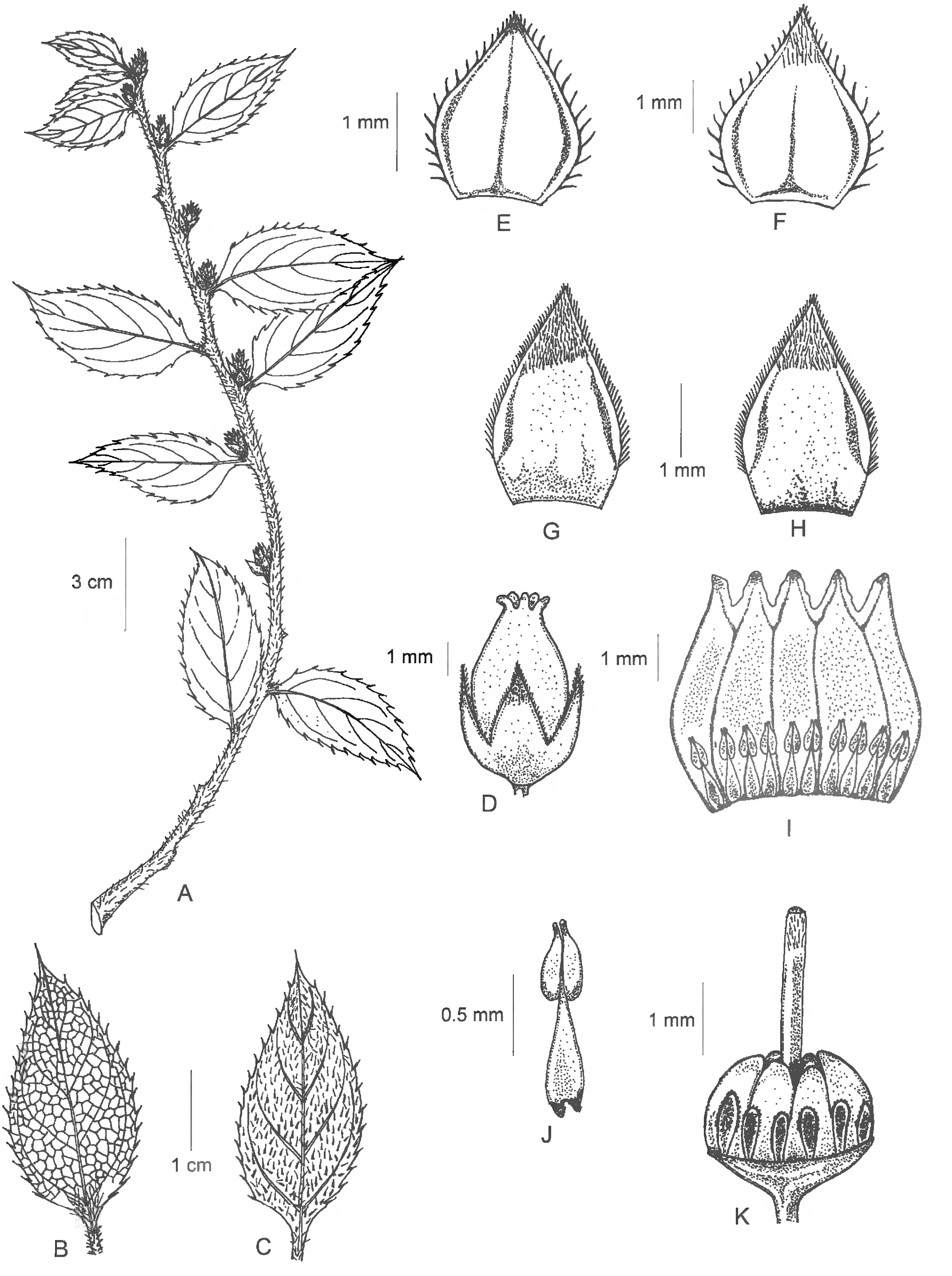

Fig. 1. ***Diplycosia indica*. A. Habit. B. Leaf, upper surface. C. leaf, lower surface. D. Flower. E. Bract. F. Bracteole. G. Calyx, dorsal surface. H. Calyx, ventral surface. I. Corolla split open. J. Stamen. K. Pistil (Scale bars: A = 3 cm; B–C = 1 cm; D – I and K = 1 mm; J = 0.5 mm).**

Table 1. Distinguishing characters of *Diplycosia indica* and *D. aperta*.

	Diplycosia indica	Diplycosia aperta
Habit	Terrestrial, prostrate shrubs	Epiphytic, sometimes scandent shrubs
Leaves	Margin with short cilia; lateral veins in 3–4 pairs, distinct beneath	Margin with long cilia; lateral veins in 2 pairs, obscure beneath
Flowers	(3–)4–6; pedicel 0.5 mm, glabrous	1 or 2, rarely 3; pedicel 0.8–1.1cm, with bristles
Bracteoles	Acute to shortly acuminate, 3–3.5 mm long, very sparsely puberulous in the apical half along midrib on dorsal surface	Obtuse, ca. 1.5 mm long, glabrous throughout the dorsal surface
Calyx	Minutely puberulous on both surfaces in apical portion	Glabrous to some fine glandular warts on dorsal surface
Corolla	ca. 4 mm long, white, lobes 0.75 mm	8–9 mm long, red or rose, lobes 1.5 mm

rounded to broadly cuneate at base, margin serrulate-ciliate with short cilia, cilia 0.5–1 mm long, laxly softly pilose at the base along mid-vein, dark green above, setulose, light green beneath; veins impressed above, distinct beneath, lateral veins in 3–4 pairs; petiole 1.5–3 mm long, setulose, red. Inflorescence a fascicle, up to 7 mm long, (3–)4–6-flowered, glabrous; bracts 1.5–2 mm long × 1.8–2.2 mm wide, basal, ovate, acute, glabrous, margin membranous, ciliate, reddish-green; bracteoles 2, 3–3.5 mm long × 1.3–1.8 mm wide, ovate, acute to shortly acuminate, opposite, concave, margin membranous, ciliate, very sparsely puberulous in the apical half along the middle on dorsal surface. Flowers 4–5 mm long, urceolate; pedicel ca. 0.5 mm long, inconspicuous, glabrous. Sepals 5–6, 1.5–3 mm long × 1–1.5 mm wide, ovate-triangular, acuminate, minutely puberulous in the apical portion on both the surfaces, margin membranous, thickly puberulous, adnate to the ovary, rosy-pink. Corolla ca. 4 mm long, urceolate, white, 6-lobed; lobes ca. 0.7 mm long, ovate, apex obtuse to rounded, margin obscurely crenulate, glabrous. Stamens 10, ca. 1.5 mm long, loosely epipetalous, caducous, filament ca. 0.8 mm long, oblong, dilated at middle, papillose; anther with tubules 0.6 mm long, very small, 2-lobed, oblong. Pistil 2.5–3.5 mm long; ovary superior, 1 mm long × 1.5 mm wide, subglobose, subglabrous or scattered puberulous, light green; style ca. 2 mm long, slender, sparsely minutely hairy in upper half; disk cupular, 8–10 lobed, pressed against the ovary, papillose. Fruit not seen.

Diplycosia indica is closely allied to *Diplycosia aperta* J.J.Sm. but can be distinguished from it by its terrestrial habit; inflorescence with 4–6, glabrous pedicelled, much smaller, white flowers; acute to acuminate, sparsely puberulous bracteoles, and puberulous calyx.

Habitat and ecology.—Rare among scrubs on sub-alpine slopes, in association with *Viburnum erubescens, Thamnocalamus aristatus,* etc. and ferns at an altitude of about 3000 m.

Flowering.—June.

Distribution.—India: Eastern Himalaya (West Bengal). Endemic.

Etymology.—*Diplycosia indica* is named after India, the country of its origin.

Conservation status.—The new species could not be traced from anywhere inside the Singalila National Park except for a small population. Since Singalila National Park—especially from Manebhanjeng to Sandakphu—is a famous trekking route, it attracts a large number of tourists and trekkers throughout the year. The increasing pressure from the tourism industry and large scale cattle grazing in and around park areas, are posing severe threats to the natural habitat of numerous species including *Diplycosia indica.*

Additional specimen examined: **INDIA. West Bengal:** Darjeeling district, 32 km N of Manebhanjeng, from Kainyakata to Kalapokhri, ca. 2950 m, 02 Jun 2006, *M.R. Debta 40813* (CAL, BSD).

ACKNOWLEDGMENTS

The authors are indebted to the director, Botanical Survey of India for providing facilities. Grateful thanks are due to G.C.G. Argent and D.J. Middleton, Royal Botanic Garden, Edinburgh for their expert suggestions

and helps, to V.J. Nair, ex-joint director, Botanical Survey of India for providing Latin diagnosis of the new species. Thanks are also acknowledged to the officials of the Forest Department, Government of West Bengal for permission to carry out research work inside the Singalila National Park and to Brijesh Kumar, Botanical survey of India, Dehradun for illustrating the new species. We greatly appreciate the helpful review of one anonymous reviewer.

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AMORPHA CONFUSA, A NEW NAME FOR AN OLD *AMORPHA* (FABACEAE: AMORPHEAE)

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ABSTRACT

A new combination, **Amorpha confusa** (Fabaceae: Amorpheae), based on *A. georgiana* var. *confusa*, is established. The variety is raised in rank due to differences in morphology, distribution, habitat preference, phenology, ploidy, and genetic variation when compared to *A. georgiana*.

RESUMEN

Se establece una combinación nueva, **Amorpha confusa** (Fabaceae: Amorpheae), basada en *A. georgiana* var. *confusa*. La variedad se promueve al rango de especie debido a las diferencias en morfología, distribución, preferencia de hábitat, fenología, ploidía, y variación genética en comparación con *A. georgiana*.

For many years, plants currently known as *Amorpha georgiana* Wilbur var. *confusa* Wilbur (Fabaceae Juss.: Amorpheae Boriss.) have been a source of taxonomic and nomenclatural confusion. Wilbur (1964) elegantly explored the intricacies of the situation in his revision of the dwarf species of *Amorpha* L. Various names often had been applied incorrectly to this species (e.g., *A. caroliniana* H. B. Croom, *A. cyanostachya* M.A. Curtis) or were unavailable (e.g., *A. glabra* Desf. ex Beadle, nom. illeg.). This left Wilbur no option but recognize it with a new name, which he did at the rank of variety due to its similarity to *A. georgiana*. At the time, this was the most conservative course of action due to the paucity of collections of both var. *georgiana* and var. *confusa*, even though Wilbur recognized that the two differed morphologically. Later, Wilbur (1975 p. 367) commented in his monograph of the genus that he remained "skeptical" that his treatment would prove "satisfactory when more is learned about them" and acknowledged that "future investigation may well demonstrate that the two taxa are specifically distinct." Most recent floristic treatments and species checklists (e.g., Isely 1990, 1998; Kartesz 1999) have followed Wilbur's treatments in recognizing two varieties. These varieties differ morphologically in many characters with var. *confusa* having larger leaflets [(10–)15–25(–35) mm long and (7–)9–15(–18) mm wide versus (3–)6–10(–15) mm long and (2–)3–5(–8) mm wide], longer petioles [(6–)8–15(–20) mm versus 1–3(–5) mm] and racemes [10–20(–30) cm versus (2–)3–5(–6) cm], less numerous leaflets, clustered, panicle-like inflorescences rather than generally solitary racemes, and bright blue rather than reddish-violet vexilla (Fig. 1; Wilbur 1964; Sorrie 1995; Weakley 1995).

Recent investigations into the current distribution, conservation status, and genetics of the two varieties have revealed additional differences and supported Wilbur's (1975) notion that they should each be recognized at the specific level. The distributions of the varieties do not overlap currently, nor did they historically based on herbarium records (Fig. 2). *Amorpha georgiana* var. *confusa* is an endemic of a few counties in

Fig. 1. a. *Amorpha confusa* at Green Swamp Preserve, North Carolina. (Photograph by Andrew Walker). b. *Amorpha georgiana* at Fort Bragg, North Carolina (Photograph by Bruce Sorrie).

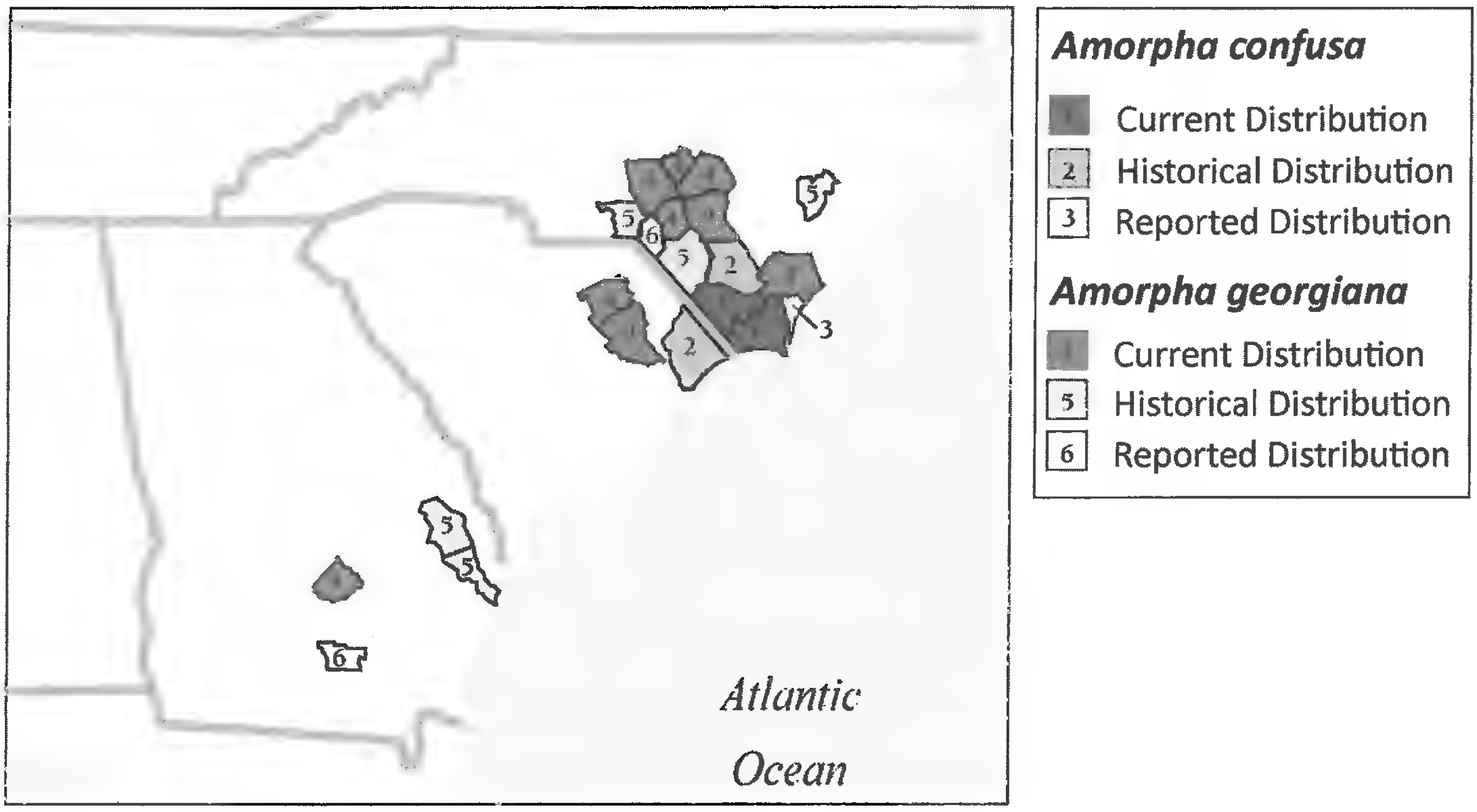

Fig. 2. Current, historical, and reported distributions by county of *Amorpha confusa* and *Amorpha georgiana* in the southeastern United States.

extreme southeastern North Carolina and immediately adjacent South Carolina, though it is now believed to be extant in only Brunswick and Columbus counties of North Carolina (Weakley 1995). *Amorpha georgiana* var. *georgiana* is found in the middle and inner Coastal Plain of North Carolina, South Carolina and Georgia (Sorrie 1995). Both varieties are associated with the longleaf pine savanna ecosystem but differ in the details of their habitat preferences with var. *confusa* occurring in flat, moist to rather dry outer Coastal Plain savannas with loamy soils, especially of the Foreston series (Weakley 1995); whereas var. *georgiana* occupies more moist to occasionally inundated areas, chiefly sandy river terraces and river banks above blackwater rivers traversing the sandhills of the middle and inner Coastal Plain, and more infrequently the edges of swampy floodplains (Sorrie 1995). Both varieties have suffered habitat loss, fragmentation, and degradation in recent years due to human activities, including fire suppression, agriculture, and land development, causing them to be of conservation concern (Sorrie 1995; Weakley 1995). In North Carolina, var. *confusa* is currently considered to be threatened (North Carolina Department of Agriculture & Consumer Services 2008) because its population numbers are estimated to be less than 14,000 individuals, and only those populations occurring in The Nature Conservancy's Green Swamp Preserve are likely to receive long-term conservation-oriented management (Weakley 1995).

The two varieties also differ in phenology, with *Amorpha georgiana* var. *confusa* flowering from late May to mid-July and var. *georgiana* flowering from late April to late May (Sorrie 1995). Additionally, recent genetic work has indicated that the genome of var. *confusa* is likely tetraploid, while that of var. *georgiana* is diploid (Straub et al. 2009). A comparison of the microsatellite variation observed for the varieties at the population level indicates that they are quite well differentiated genetically and preliminary phylogenetic analyses of chloroplast spacer region and low-copy nuclear gene DNA sequence data indicate that they are likely not each other's closest relative among *Amorpha* species (S. Straub & J. Doyle, unpublished data).

Since the time of Wilbur's (1964) original publications, additional studies of the morphology, distributions, habitat preferences, phenology, and genetics of the two varieties have shown the extent to which they are distinct from one another. These differences warrant the recognition of var. *confusa* at the rank of species (Sorrie 1995; Weakley 1995). Recognition at this rank further emphasizes the conservation importance and need of both of these imperiled species.

Amorpha confusa (Wilbur) S.C.K. Straub, Sorrie & Weakley, comb. et stat. nov. *Amorpha georgiana* var. *confusa* Wilbur, J. Elisha Mitchell Sci. Soc. 80: 58. 1964. Type: UNITED STATES. NORTH CAROLINA. Brunswick Co.: Savannah, 7 mi SW of Wilmington, 31 May 1938, *R.K. Godfrey & I.V. Shunk 4122* (LECTOTYPE, designated by Wilbur 1975: GH, digital image!; DUPLICATE OF THE LECTOTYPE: US, digital image!).

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Wilbur (1964) did not choose among the two syntypes listed in the protologue as the holotype, although he later indicated that he considered the specimen at GH to be the holotype (Wilbur 1975: 366), here corrected to lectotype pursuant to Article 9.8. of the ICBN (McNeill et al. 2006).

Additional collections. **NORTH CAROLINA. Bladen Co.:** pinewoods, *Biltmore Herbarium 5767B* (NY). **Brunswick Co.:** pineland near Wilmington, 28 Aug 1938, *R.K. Godfrey 6233* (GH, US, NCSC-4939); oak woods along route 17 about 3.5 mi NE of Bolivia, 22 Jun 1947, *C.E. Wood, Jr. & I.D. Clement 7054* (GH, NCU-175175); dry sandy pineland, 20 mi S of Wilmington on route 17, 27 Jun 1950, *F.H. Sargent 10008* (GH); scrub oak sand ridge between Shallotte and Ash, 6 Jul 1951, *R.K. Godfrey & H.L. Blomquist 51177* (FLAS, NCSC); dry, sandy soil, savanna, 2.4 mi W of Shallotte, Highway 130, 10 Jul 1951, *H.L. Blomquist, R.K. Godfrey & R.L. Wilbur15225* (DUKE); infrequent in weedy ditch about 1 mi W of Shallotte on NC 130; 6 Jun 1957, *R.L. Wilbur 5991* (DUKE-141703); infrequent on sandy disturbed roadside about 6 mi NW of Southport on Route 87, 12 Jun 1957; *R.L. Wilbur 6169* (DUKE-141699); pine flatwoods about 4 mi from Southport on route 87-133, 10 Jul 1963, *R.L. Wilbur 6954* (DUKE, FSU); open piney woods about 11 mi NW of Supply on Route 211, 18 Aug 1967, *R.L. Wilbur 9466* (DUKE-186242); powerline right-of-way, junction of state roads 1518 and 1521, N of Funston,14 Jun 1979, *D.J. Sieren 1835* (NCU-551161, WILM-14283); pine/wiregrass savanna 0.8 km SE of borrow pit on east side of NC 211, 9.4 km N of US 17, 18 Jul 1986, *J.B. Taggart 224* (NCU-557630); Green Swamp Preserve, 5.5 mi N of Supply, 22 May 2003, *A.S. Weakley & G.T. Chandler 7242* (NCU-569103, NCU-569104, NCU-569106); Green Swamp Preserve, W of Big Island Savanna, 22 May 2003, *A.S. Weakley & G.T. Chandler 7244* (NCU-569107, NCU-569109, NCU-569111); Boiling Springs Lake Preserve, Camp Pretty Pond Quad, 11 Aug 2006, *J.C. Morris 081106-11* (NCU-584945, WILM). **Columbus Co.:** low woods, Nakina, 25 Jun 1935, *P.O. Shallert s.n.* (GH), railroad savannah near Route 76, 1 mi SE of Delco, 31 Jul 1949, *W.B. Fox & R.K.Godfrey 2874* (NCSC-34075); savanna 3.7 mi NW of Old Dock on NC 130, 2 Jul 1968, *S.W. Leonard & K. Moore 1720* (FLAS, FSU, GH, NCU-319790); sandy damp soil along CR 1928 to Shulkins, 7 Jul 1989, *J.A. Churchill 89–685* (VDB). **New Hanover Co.:** Wilmington, 1 Jul 1904, *Biltmore Herbarium 1391-L* (NCU); Wilmington, 6 Oct 1908, *E.A. Bartram s.n.* (PH); Wilmington, 11 Jun 1917, *T.G. Harbison 3415* (NCU-3469); low swampy ground, Wilmington, 11 Jun 1917, *T.G. Harbison 16* (A). **SOUTH CAROLINA. Horry Co.:** 9 mi S of Green Sea, 16 Jun 1941, *H.R. Totten s.n.* (NCU-22550, NCU-577773).

ACKNOWLEDGMENTS

The authors thank the curators of A, DUKE, FLAS, FSU, GH, HUH, NCSC, NCU, US, VDB and WILM for access to specimens and digital images, the North Carolina Natural Heritage Program for access to locality data, James L. Reveal (BH) for helpful discussions related to nomenclature issues, and James L. Reveal and Guy Nesom for valuable comments which improved the manuscript. The authors acknowledge funding from the the U.S. Fish and Wildlife Service for status surveys, a Garden Club of America Catherine H. Beattie Fellowship to S.C.K.S., and National Science Foundation grant DEB-0709960.

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BOOK REVIEW

Michael Wink and Ben-Erik van Wyk. 2008. **Mind-Altering and Poisonous Plants of the World.** (ISBN-13 978-0-88192-952-2, hbk.). Timber Press Inc., 133 S.W. Second Avenue, Suite 450, Portland, Oregon 97204-3527, U.S.A. (**Orders:** www.timberpress.com, mail@timberpress.com, 800-327-5680, 503-227-3070 fax). $49.95, 464 pp., color throughout, black/white illustrations, 6 5/8" × 9 1/2".

Mind-Altering and Poisonous Plants of the World is a fascinating book. Its subtitle—*A scientifically accurate guide to 1200 toxic and intoxicating plants*—is a perfect description of this delightful and useful book. Having given regular lectures on poisonous plants, I have found this book to be a valuable and reliable source of information on poisonous plants. Not only is this book for the botanist, but a variety of audiences would find it meaningful to own: farmers, ranchers, teachers, students, homeowners, gardeners, horticulturists, florists, botanists, chemists, medical and law enforcement personnel, health care professionals, parents, and anyone with a curiosity in the power of green plants.

It has been said, "Poisons, those subtle and silent weapons capable of destroying life mysteriously—secretly and without violence—have ever had a peculiar fascination for mankind." Poisons and poisonous plants certainly fascinated the authors, Wink and van Wyk; they have done a spectacular job in assimilating a vast amount of information into a practical and user friendly format. Beautiful but poisonous plants are often used as garden ornamentals, potted plants, even florist flowers, yet most people are unaware of the dangers posed by the toxins derived from them. *Mind-Altering and Poisonous Plants of the World* takes you on a journey though the historical and modern day uses of these toxic plants. The introduction is followed by the "guts" of the book, an alphabetical list of about 200 plants. In the authors' words, "About 200 of the most relevant poisonous and mind-altering plants are characterized by concise monographs. Essential facts about another 1000 species are provided in the 'Quick guide to poisonous and mind-altering plants' at the end of the book." Each poisonous plant monograph is organized in 12 sections: **1)** Name, **2)** plants with similar properties, **3)** plant characters, **4)** occurrence, **5)** classification, **6)** active ingredients, **7)** utilization, **8)** toxicity, **9)** symptoms, **10)** pharmacological effects, **11)** first aid, and **12)** systematics. Beautiful color photographs with critical information accompany each monograph.

Take note, accidental poisonings happen and therefore I was delighted to see a list of suggestions of how to avoid poisoning or to help poison center personnel in case of ingestion of a toxic plant. The Toxic Exposure Surveillance System data for 2006—from the American Association of Poison Control Centers' National Poison Data System—show plants accounted for 2.7% of the substances most frequently (64,236 cases) involved in human exposures. Sadly, deaths do occur. I looked throughout the book but couldn't find the nationwide Poison Help line number (1-800-222-1222). This toll-free number is available 24 hours a day and will connect you to the nearest poison center wherever you are calling from in the United States. In an emergency call 9-1-1. Increase your knowledge of toxic plants, know what to do in case of suspected poisoning, and discover the most important factor in poisoning prevention, plant identification, with this book. Plant names and accurately identifying plants have practical uses after all. Maybe you can help prevent an emergency or even save a life. In case of poisoning always consult a medical professional or qualified practitioner. *Mind-Altering and Poisonous Plants of the World* has a **Warning and Disclaimer** on the copyright page, but I think it is still a good investment at $49.95.—*Barney Lipscomb, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

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A NEW COMBINATION IN NORTH AMERICAN *TEPHROSIA* (FABACEAE)

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ABSTRACT

Tephrosia ×intermedia (Small) G.L. Nesom & Zarucchi, comb. nov., is the correct name for plants regarded as hybrids between *Tephrosia chrysophylla* and *T. florida*, replacing *T. ×floridana* (Vail) Isely. Details of typification are given for *Cracca intermedia* Small and *Cracca floridana* Vail.

RESUMEN

Tephrosia ×intermedia (Small) G.L. Nesom & Zarucchi, comb. nov., es el nombre correcto para las plantas consideradas como híbridos entre *Tephrosia chrysophylla* y *T. florida*, que reemplaza a *T. ×floridana* (Vail) Isely. Se aportan detalles de la tipificación de *Cracca intermedia* Small y *Cracca floridana* Vail.

Cracca intermedia Small was described (Small 1894) as a new species intermediate between *C. chrysophylla* (Pursh) Kuntze (= *Tephrosia chrysophylla* Pursh) and *C. ambigua* (M.A. Curtis) Kuntze (= *Tephrosia florida* (F. Dietr.) C.E. Wood). Vail (1895) curiously provided *C. intermedia* with a new name, *Cracca smallii* Vail, because she apparently regarded *C. intermedia* as invalidated by the earlier *Tephrosia intermedia* Graham in Wall. In the same publication, Vail described *C. floridana* Vail, noting that it was "very close" to *C. smallii*. Isely (1982, 1990, 1998) provided the combination *Tephrosia ×floridana* (Vail) Isely and used it in reference to the putative *T. chrysophylla*—*T. florida* hybrids, even though he correctly recognized Graham's *T. intermedia* to be a nomen nudum.

Tephrosia intermedia Graham was indeed published without a description and is illegitimate as a nomen nudum, but it does not block the transfer of *Cracca intermedia* Small to *Tephrosia*. Many of the nomina nuda in Wallich's list were validated by description in Don (1831–1834), but *Tephrosia intermedia* is not among them. "T. intermedia Grah. in Wall. Cat. 5632" was listed at the end of the paragraph for *Tephrosia tinctoria* Pers. var. *intermedia* [W & A.] in J.D. Hooker, Fl. Brit. India 2:112. 1879, so the epithet "*intermedia*" at the rank of species under "*Tephrosia*" was not there validated.

Tephrosia ×intermedia (Small) G.L. Nesom & Zarucchi, comb. nov. *Cracca intermedia* Small, Bull. Torrey Bot. Club 21:303. 1894 (non *Tephrosia intermedia* Graham [nom. nud.], Numer. List [Wallich] n. 5632. Between 1831 and 1832,). *Cracca smallii* Vail, Bull. Torrey Bot. Club 22:33. 1895 [nom. nov. for *C. intermedia* Small]. *Tephrosia smallii* (Vail) B.L. Rob., Bot. Gaz. 28:198. 1899. Type: U.S.A. Florida. [Duval Co.]: near Jacksonville, Florida, 31 May, Fr. 11 Jul 1893, *A.H. Curtiss 4231* (lectotype: NY 00006579, digital image!; isolectotypes: NY 00006578, digital image!; US, US-digital image!). Small's protologue noted that the collection was made "by Mr. A.H. Curtiss in 1893, flowering on May 31st and in mature fruit on July 11th" and that it was collected from "dry and poor 'Blackjack thickets' about Jacksonville," although the habitat information does not appear on the label of any of the specimens. Isely (1982) indicated "*Curtiss 4231*" at NY to be the "holotype" but he did not specify which of the duplicates was the type. Sheet 00006579 has a printed label "type" while 00006578 has a printed label "isotype," and it is assumed here that these labels are correct designations. The label of 00006578 has "*C. smallii* A.M. Vail" handwritten below the typed "*Cracca intermedia* Small. sp. nov."

Cracca floridana Vail, Bull. Torrey Bot. Club 22:35. 1895. *Tephrosia ×floridana* (Vail) Isely, Brittonia 34:340. 1982. Type: U.S.A. Florida. Lake Co.: high pineland, vicinity of Eustis, Jul 1894, *G.V. Nash 1198* (lectotype, designated by Isely 1982: NY, digital image!). Vail cited "Central Florida, G.V. Nash Nos. 494½, 1198, 1263, 1334, 1552, 1615. Louisiana, New Orleans, Dr. Ingalls. Types in Herb. Columbia College." Photos of all syntypes except *Nash 1334* are displayed on the NY web site. As noted by Isely (1982), the Ingalls collection does not appear to represent a different taxon.

The original hypothesis of hybrid origin of *Tephrosia intermedia* has been accepted by those who have further studied the genus (Vail 1895; Robinson 1899; Wood 1949). Isely (1998, p. 856–857) noted that "As alleged

by Wood (1949), *Tephrosia ×floridana* probably is a derivative of hybridization between *T. chrysophylla* and *T. florida*. Whatever its origin, it is sufficiently widely distributed and consistent in characters to deserve binomial listing." It has been collected from Alabama, Florida, Georgia, and Mississippi, but the distribution is sporadic and its origin as a recurrent hybrid seems a reasonable hypothesis. It occurs in association with the two putative parents and is intermediate in morphology.

ACKNOWLEDGMENTS

We are grateful to Kanchi Gandhi (GH) and Richard P. Wunderlin (USF) for comments and analysis.

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A RECOMBINATION FOR VARIETIES OF *ANTICLEA ELEGANS* (MELANTHIACEAE)

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ABSTRACT

The new combination is here made for **Anticlea elegans** var. **glaucus,** formerly within the polyphyletic *Zigadenus* complex as *Zigadenus elegans* var. *glaucus*.

RESUMEN

Se hace una nueva combinación para **Anticlea elegans** var. **glaucus,** previamente incluida en el complejo polifilético *Zigadenus* como *Zigadenus elegans* var. *glaucus*.

Based on molecular and morphological data (Zomlefer et al. 2001), the authors made recombinations at the generic and species-level for taxa of the former *Zigadenus* complex (Zomlefer & Judd 2002). While assisting in the update of these taxa for the *Plants Database* (USDA–NRCS 2009) for the National Resources Conservation Service (Cooperative Agreement 68-3H75-3-122 Mod 14; PI Craig C. Freeman, KANU), the first author realized the necessity of making the following infraspecific transfer to *Anticlea elegans* (formerly *Zigadenus elegans*), presented below.

Anticlea elegans (Pursh) Rydb. var. **glaucus** (Nutt.) Zomlefer & Judd, comb. nov. Basionym: *Melanthium glaucum* Nutt., Gen. 1:232. 1818.

Zigadenus elegans Pursh var. *glaucus* (Nutt.) Preece ex Gleason & Cronq. Man. Vasc. Pl. NorthE. U.S. Canad., ed. 2, 864. 1991.

The wide-ranging *Anticlea elegans* (Alaska–Canada south to northern Mexico), occurs in various habitats: generally bogs, beaches, and calcareous wetlands in eastern North America, and prairies, coniferous forests, and alpine meadows in the west (Zomlefer 1997). The differences between the eastern element, *A. elegans* var. *glaucus* (plants glaucous; leaves blunt or subacute, coriaceous; inflorescence usually paniculate; bracts herbaceous, subulate; tepals intensely colored; capsule ovoid-conic), and the western *A. elegans* var. *elegans* (plants green; leaves pointed, more herbaceous; inflorescence usually racemose; bracts scarious margined; tepals pale; capsule lance-conic), as outlined by Fernald (1935), are most evident in the geographical extremes (Preece 1956), and these two taxa require further study in their area of morphological integradation in the eastern Dakotas–western Minnesota region (Gleason & Cronquist 1991; Schwartz 2002). Varietal recognition is appropriate given our current understanding of the pattern of variation.

ACKNOWLEDGMENTS

We thank Fred Barrie and Guy Nesom for their careful check of this nomenclatural note.

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TAXONOMIC OVERVIEW OF *EURYBIA* SECT. *HERRICKIA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Herrickia horrida and five closely related species are included here within *Eurybia* sect. *Horrida*. These species are *E. glauca*, *E. horrida*, *E. pulchra*, and *E. wasatchensis*, as previously treated by Nesom, and two other species recently recognized by molecular evidence as close relatives: **Eurybia kingii** (D.C. Eat.) G.L. Nesom, comb. nov. (including **Eurybia kingii** var. **barnebyana** (Welsh & Goodrich) G.L. Nesom, comb. nov.) and **Eurybia aberrans** (A. Nels.) G.L. Nesom, comb. nov. The first five of these species were treated by Brouillet as a broadened genus *Herrickia*; the last was segregated as the monotypic genus *Triniteurybia* Brouillet, Urbatsch & Roberts. Molecular data indicate that *Eurybia*, *Herrickia*, and *Triniteurybia* constitute a 3-taxon grade at the base of the Machaerantherinae clade but morphological distinctions of *Herrickia* and *Triniteurybia* from *Eurybia* are trivial or non-existent and their separation from *Eurybia* at generic rank is based strictly on cladistic hypotheses. Nomenclatural summaries and geographic distributions are shown for the six species of *Eurybia* sect. *Herrickia*.

RESUMEN

Herrickia horrida y cinco especies muy relacionadas con ella se incluyen aquí en *Eurybia* sect. *Horrida*. Estas especies son *E. glauca*, *E. horrida*, *E. pulchra*, y *E. wasatchensis*, tal como habían sido tratadas previamente por Nesom, y otras dos especies reconocidas recientemente mediante pruebas moleculares como parientes próximos: **Eurybia kingii** (D.C. Eat.) Nesom, comb. nov. (que incluye **Eurybia kingii** var. **barnebyana** (Welsh & Goodrich) Nesom, comb. nov.) y **Eurybia aberrans** (A. Nels.) Nesom, comb. nov. Las cinco primeras especies fueron tratadas por Brouillet como el género más amplio *Herrickia*; la última fue segregada como el género monotípico *Triniteurybia* Brouillet, Urbatsch & Roberts. Los datos moleculares indican que *Eurybia*, *Herrickia*, y *Triniteurybia* constituyen un grado de tres taxa en la base del clado Machaerantherinae pero las diferencias morfológicas de *Herrickia* y *Triniteurybia* con *Eurybia* son triviales o inexistentes y su separación de *Eurybia* en el rango genérico está basada estrictamente en hipótesis cladísticas. Se aportan resúmenes nomenclaturales y distribuciones geográficas para las seis especies de *Eurybia* sect. *Herrickia*.

Prior to 1994, *Herrickia horrida* Woot. & Standl. either had been maintained as a monotypic genus or treated as *Aster horridus* (Woot. & Standl.) Blake. Nesom (1994) united it with three morphologically similar species in the western U.S.A. and treated the group as sect. *Herrickia* (Woot. & Standl.) Nesom of the genus *Eurybia* (Cassini) S.F. Gray: *Eurybia glauca*, *E. horrida*, *E. pulchra*, and *E. wasatchensis*. *Eurybia* in the sense of the present overview includes a total of 28 species distributed over eastern and western North America.

Based on molecular study, Brouillet et al. (2004) reinstated *Herrickia* Woot. & Standl. at generic rank, including the species noted above but reducing *Eurybia pulchra* to varietal rank within *Herrickia glauca* and expanding the group to include *Aster/Tonestus kingii*. They also discovered *Haplopappus/Tonestus aberrans* to be a close relative of *Herrickia* and *Eurybia* and segregated it as the monotypic genus *Triniteurybia* Brouillet, Urbatsch & Roberts (Brouillet et al. 2004). Molecular evidence indicates that this group of "herrickioid" taxa forms a grade at the base of subtribe Machaerantherinae: *Oreostemma* (*Herrickia* (*Eurybia* (*Triniteurybia* (*Machaerantherinae*)))) (Brouillet et al. 2004, from ITS and 3'ETS nrDNA; Selliah and Brouillet 2007, from the nuclear CNGC4 gene). The boundaries of *Eurybia* were further adjusted with the transfer of *Eurybia* (*Aster*) *pygmaea* (Lindl.) Nesom and *Eurybia* (*Aster*) *chapmanii* (Torrey & A. Gray) Nesom to *Symphyotrichum* (Brouillet & Selliah 2005; Brouillet et al. 2006).

The taxonomic repositioning of *Symphyotrichum chapmanii* and *S. pygmaea* is justified, based on molecular as well as morphological criteria, and those two species are outside of the immediate relationship of the species of *Herrickia/Eurybia/Triniteurybia*. The inclusion of *Aster kingii* and *Haplopappus aberrans* in this group of species also is a valuable and morphologically justified insight. The implicit rationale of strict monophyly, however, for recognizing three separate genera among these few species of the eurybioid grade

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is based on a philosophical position not universally shared by systematists (e.g., Nordal & Stedje 2005), whether or not further molecular data may confirm the pattern of cladistic relationship among them. There is no consistent, diagnostic morphological difference to separate *Herrickia* (sensu Brouillet) from *Eurybia*, and *Triniteurybia* is distinguished from *Herrickia* and *Eurybia* by a single feature (lack of ray florets), which is sometimes variable within species and at most no greater than sometimes differentiating species among genera of Machaerantherinae sensu stricto. Of course, as among species, there are no consistent or objective criteria specifying the number or kinds of differences that justify the recognition of closely related genera (or see McVaugh's set of recommended criteria [1945]). Similarly, however, there is no constraint that the pattern of descent be mirrored in nomenclature that does not account for phenotypic modification (or lack of it). Were *Herrickia*, *Eurybia*, and *Triniteurybia* distinguished by significant morphological features, combined with a preliminary cladistic hypothesis, their treatment as separate genera would certainly be justified.

The present overview examines the generic concepts of *Herrickia*, *Eurybia*, and *Triniteurybia* and shows geographical distributions of species included here within *Eurybia* sect. *Horrida*. Map data are taken from specimens at ASC, BRIT-SMU, MO, SJC, and TEX-LL.

Morphological distinction of *Herrickia* from *Eurybia*

Eurybia (sensu Nesom 1994, 2000) is distinctive in its combination of corymboid inflorescence, ciliate-fringed, rounded phyllaries with a green, often basally truncate apical patch, linear-lanceolate disc style appendages, cylindric and multinerved cypselae, 2-seriate pappus of equal-length, apically thickened bristles, and base chromosome number of $x = 9$. Brouillet et al. (2004, 2006) did not provide morphological criteria for the distinction of *Herrickia* from *Eurybia*, but for the FNANM treatment, the key to genera (FNANM Editorial Committee 2006, p. 19) used the following contrast.

1. Stems and leaves usually stipitate-glandular, sometimes eglandular and glaucous; leaves mostly cauline, entire or spinulose-serrate, glabrous or scabrellous; phyllaries sometimes rounded, usually keeled, apices acute to long-acuminate; rays 8–27; disc corolla tubes shorter than limbs (w Cordilleras) ____ **Herrickia**
1. Stems and leaves usually eglandular, sometimes stipitate-glandular (e North America only), not glaucous; leaves basal and/or cauline, serrate (teeth sometimes spinulose or spinose, blades then linear, grass-like, se North America) or entire, hairy or glabrous; phyllaries usually rounded, sometimes keeled, apices obtuse to acute; rays 5–60; disc corolla tubes shorter or longer than limbs ____ **Eurybia**

Each of the comparisons in the key shows broadly overlapping characters and there is no consistent, diagnostic morphological difference to separate *Herrickia* (sensu Brouillet) from *Eurybia*.

My rationale for the recognition of sect. *Herrickia* (Nesom 1994) was similarly lacking in diagnostic cohesiveness, reflecting more a perception of the geographical coherence of the species. *Eurybia horrida* and *E. wasatchensis* are similar in their subshrubby habit, sessile and subclasping leaves, subequal phyllaries, and tendency to produce foliaceous bracts immediately subtending the involucre. *Eurybia glauca* and *E. pulchra* are similar to the former two in habit and subclasping leaves but differ in graduate phyllaries and lack of foliaceous bracts. Only the subshrubby habit is distinct among other species of the genus and *E. glauca* and *E. pulchra* sometimes are more herbaceous than subshrubby. *Tonestus aberrans* and *Aster kingii* are similar between themselves (see comments below) and both show features of *Eurybia*, but they are distinct from other "herrickioids" in their herbaceous habit and reduced inflorescence; both produce non-clasping leaves and graduate phyllaries, and they lack foliaceous bracts. Thus, there apparently is no obvious morphological feature diagnostic of the herrickioid group, but the seemingly interrelated species clusters and their geographic coherence (Figs. 1 and 2) suggest that they are closely related within the larger *Eurybia*, and molecular data tentatively confirm this.

Morphological distinction of *Eurybia* and *Triniteurybia*

In the original description of *Triniteurybia* as a new genus (Brouillet et al. 2004), its diagnostic features were noted (in the Latin diagnosis only, as differences from *Eurybia*) as eradiate heads and stipitate-glandular leaves. The western U.S.A. species *Eurybia integrifolia* and *E. conspicua*, however, have stipitate-glandular foliage, as does *Herrickia* (*Eurybia*) *horrida*. *Herrickia glauca* var. *pulchra* (= *Eurybia pulchra*), *Herrickia* (*Eu-

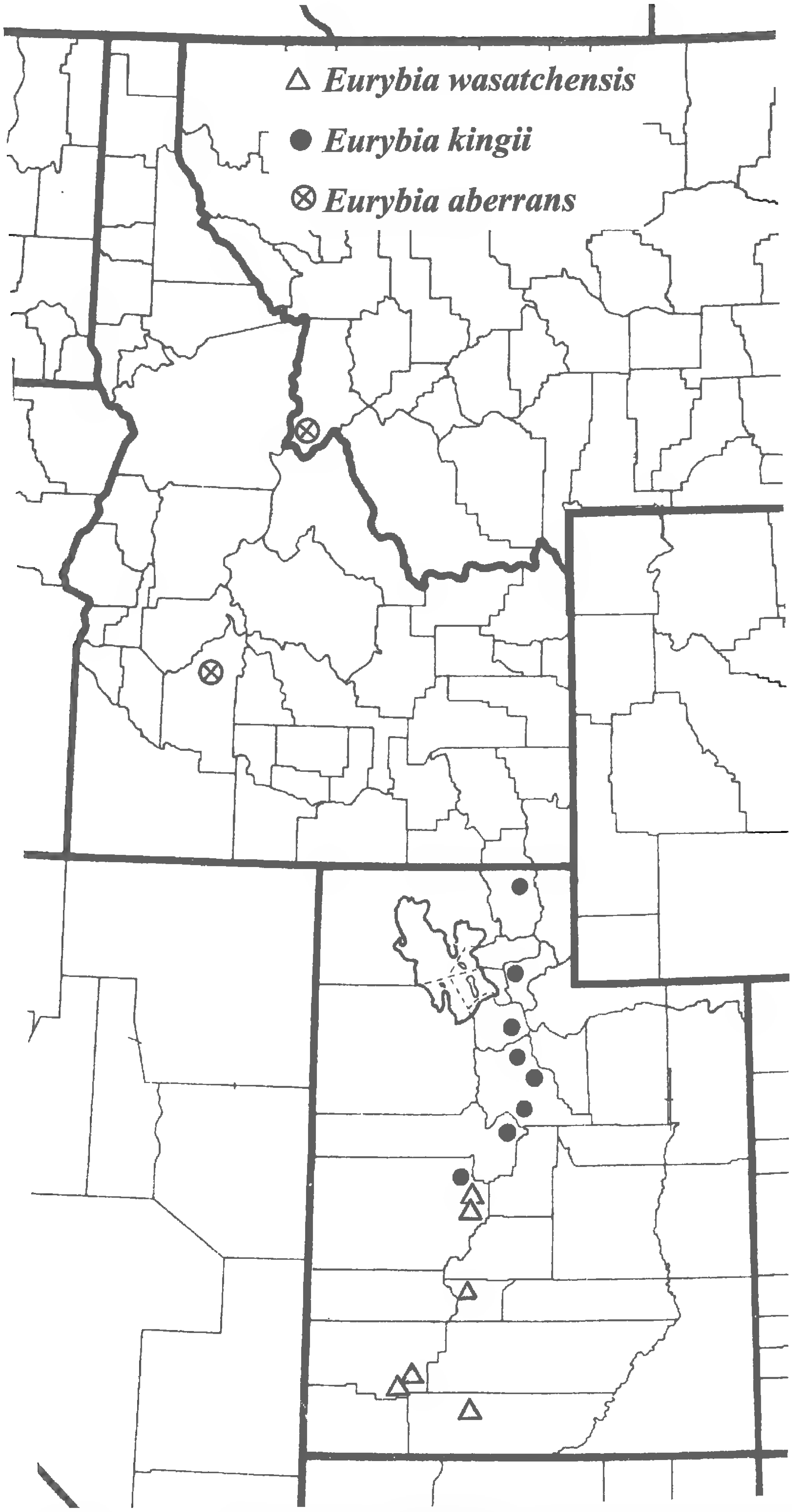

Fig. 1. Distribution of *Eurybia wasatchensis, E. kingii,* and *E. aberrans.*

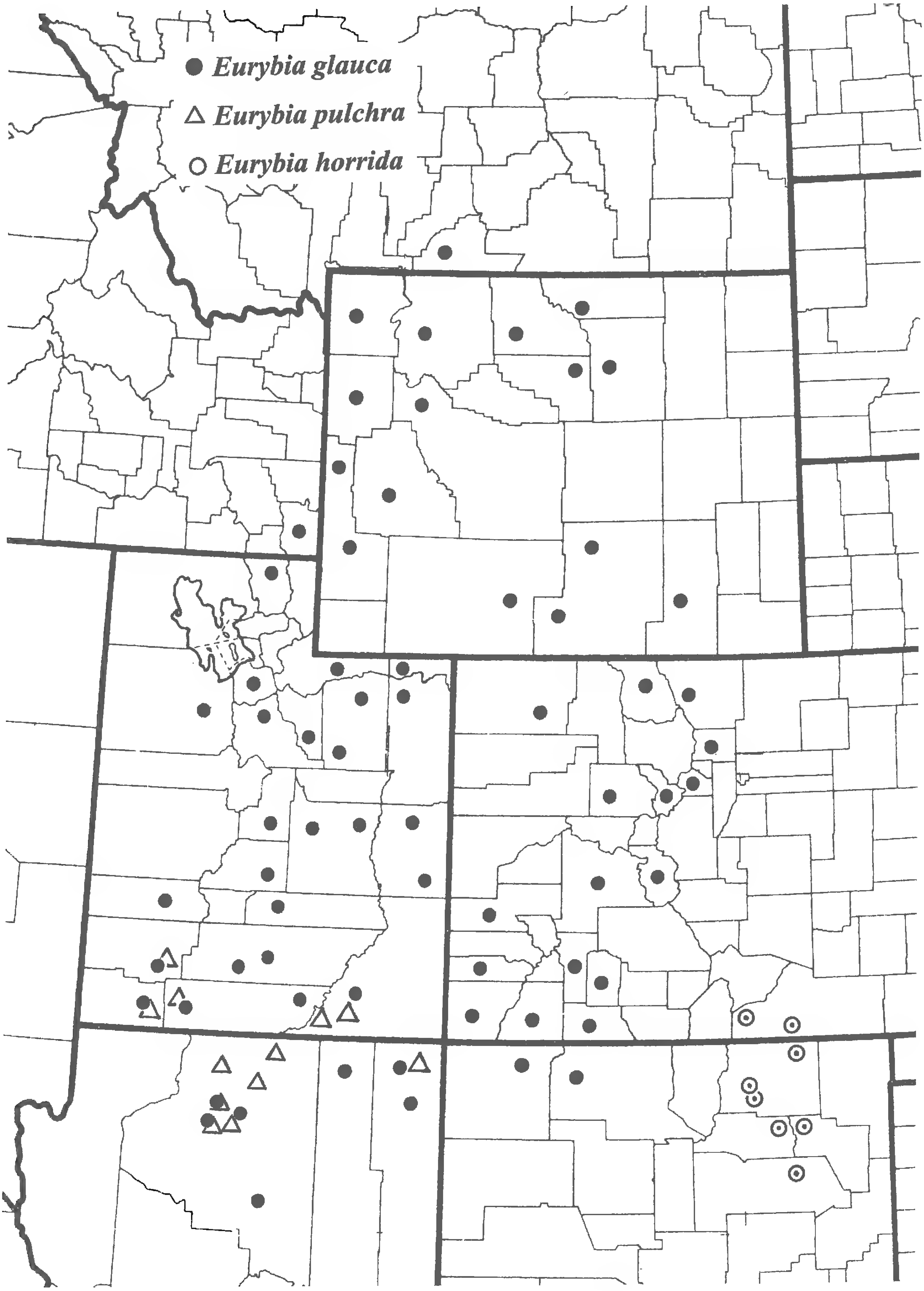

FIG. 2. Distribution of *Eurybia glauca* and *E. pulchra*, and *E. horrida*. The record for *E. pulchra* in Iron Co., Utah, is based on the citation by Welsh (2003).

rybia) *wasatchensis*, and the recently joined *Herrickia kingii* have stipitate-glandular stems, peduncles, and phyllaries. Distal leaves of *H. kingii* sometimes are minutely stipitate-glandular (e.g., *Smith 3508*, TEX, from Box Elder Co., Utah). Some species of *Eurybia* in the eastern U.S.A. also produce stipitate-glandular vestiture: e.g., *E. macrophylla*, *E. schreberi*, *E. spectabilis*. In summary, the vestiture of *Triniteurybia aberrans* is not distinct among its close relatives. Brouillet later observed (2006, p. 364) that stipitate-glandularity "is most likely a shared primitive feature within [*Herrickia*] and is therefore not indicative of a particular relationship within the group."

In the FNANM treatment of *Triniteurybia*, Brouillet (2006, p. 382) observed that "the cylindro-campanulate heads with imbricate phyllaries and a wide green area, and the coarse, dentate foliage, are similar to those of *Eurybia*. The lack of ray florets clearly distinguishes *Triniteurybia*." In fact, lack of rays has been the only morphological feature noted in any discussion that is diagnostic of the new genus. *Triniteurybia aberrans* is the only rayless species in the eurybioid grade, but within subtribe Machaerantherinae sensu stricto, *Dieteria canescens* is variable in ray production, *Arida carnosa* is rayless, and *Xanthisma grindelioides* is rayless. Ray production also is variable among species of *Grindelia*. Lack of ray florets may justify recognition of a taxon at specific rank, but there is no other example in the Astereae where it is the sole morphological character for distinction of a genus.

Eurybia kingii and Eurybia aberrans

In the positioning of *Aster kingii* within *Tonestus* (Nesom 1991), the species was noted (p. 124) to be most closely similar to *Tonestus aberrans*: "Indeed, as a pair the two are somewhat set apart from the rest of the genus in the toothed leaves often with spinulose teeth, narrowly lanceolate-attenuate and apically spreading or reflexed phyllaries, style appendages with more widely arranged sweeping hairs, and purplish disc corolla lobes." And (p. 125) "in spite of its white rays, it fits more securely in [*Tonestus*] than in *Aster*, particularly when placed next to *T. aberrans*." Molecular evidence confirms that the two are closely related, and their morphological and geographical similarity (Fig. 1) support this hypothesis. Both are treated here within *Eurybia*.

Taxonomic status of *Aster glaucodes* subsp. *pulcher* Blake

Nesom (1994) treated *Aster glaucodes* subsp. *pulcher* at specific rank within *Eurybia*, as *E. pulchra*, distinct from *E. glauca*. *Eurybia pulchra* "differs from *E. glauca* in its smaller leaves, apically acute phyllaries, and well-developed glandularity. ... *Eurybia pulchra* has a restricted geographic range, and in the specimens I have examined, there appears to be no intermediacy between it and *E. glauca*" (p. 194). The present study shows that *E. pulchra* (northern Arizona and southern Utah) is sympatric with the more widespread *E. glauca* (Fig. 2) and confirms a paucity of intermediates between them. Plants of *E. pulchra* have distal stems, peduncles, and phyllaries densely stipitate-glandular, while those of *E. glauca* are completely glabrous.

Numerous collections of both taxa have been made in the Grand Canyon, in the area of Havasupai Canyon and roughly between Havasupai Canyon and Bright Angel Canyon, e.g.: **Eurybia glauca:** *Clover 4513, 5136, 7018* (LL), *Deaver 1524, 2135, 2677, 2944, 3053* (ASC), *Hodgson 16026* (ASC); **Eurybia pulchra:** *Clover 7189* (LL), *Deaver 3042* (ASC), *Rink 4455, 4477a* (ASC), *Stevens s.n.* [14 Aug 1992], *s.n.* [27 Sep 1992] (ASC). Among all plants I have studied, the only three that might suggest the possibility of gene flow are from this area: *Watters 26* (ASC) and *Deaver 4412* (ASC) are typical *E. glauca*, except that the peduncles of each are minutely and sparsely glandular for about one centimeter immediately below the heads; *Stevens s.n.* [10 Apr 1991] (MO) is glabrous except for sparsely glandular distal peduncles and glandular phyllary margins.

A putative distinction noted by Brouillet et al. (2006) in number of disc florets (12–32 in *Eurybia glauca*, 29–40 in *E. pulchra*) is not confirmed here, as *E. pulchra* has florets evenly distributed in number down to at least 19. Leaf and phyllary morphology also overlap, though *E. pulchra* does tend to have slightly smaller leaves and more acute phyllaries. Within the area of sympatry, differences in habitat and phenology are not apparent.

In his decision to treat *Eurybia pulchra* at varietal rank within *E. glauca*, Brouillet (2003, p. 1561) noted that "the ranges of the two taxa appear to be parapatric in southern Utah-northern Arizona, with *E. pulchra* restricted to the vicinity of the Grand Canyon while *E. glauca* ranges widely to the north and east into the Southern Rocky Mountains; it must be noted however, that populations of the latter are found in Arizona south and east of the Grand Canyon. Nonetheless, no mixed population of the two taxa has been reported. The restricted range and distinct glandularity justify that *E. pulchra* be recognized as a taxon. Nevertheless, glandularity alone does not seem to justify recognizing *E. pulchra* as a distinct species." Brouillet's observation that the lack of glands in *E. glauca* represents a derived condition is reasonable and probably correct but in itself not pertinent to the decision of rank. The contrasting observation here that the ranges are sympatric suggests that the distinct polarity in vestiture is maintained through genetic isolation, in which case specific rank for each entity is justified. It is possible that in the southern part of the range (the range of *E. pulchra*), some kind of genetic switching turns on or off the expression of glands, but similar variation does not occur within other taxa of sect. *Herrickia* or any other *Eurybia* species. If *E. pulchra* is to be recognized at any rank above "forma," the behavior of these two taxa as distinct species is the simplest hypothesis as the basis for assignment of rank. Field study clearly is needed.

Welsh (2003) recognized the distinctiveness of *Eurybia puchra* and treated it as a variety of *E. wasatchensis* rather than a closer relative of *E. glauca*. The implication by Brouillet et al. (2006) that *E. pulchra* and *E. glauca* are sister taxa is better supported by morphology.

TAXONOMIC SUMMARY OF *EURYBIA* SECT *HERRICKIA*

Eurybia sect. **Herrickia** (Woot. & Standl.) Nesom, Phytologia 77:258. 1994. *Herrickia* (Woot. & Standl.). *Triniteurybia* Brouillet, Urbatsch & Roberts, Sida 21:898. 2004.

Lack of a clear diagnosis for the herrickioid group, apart from the seemingly interrelated species clusters and the geographic coherence of the species, renders the formal recognition of sect. *Herrickia* weakly justified. Nevertheless, it is a useful category in reference to the group.

1. Eurybia aberrans (A. Nels.) G.L. Nesom, comb. nov. Basionym: *Macronema aberrans* A. Nels.; *Haplopappus aberrans* (A. Nels.) H.M. Hall; *Sideranthus aberrans* (A. Nels.) Rydb.; *Tonestus aberrans* (A. Nels.) Nesom & Morgan; *Triniteurybia aberrans* (A. Nels.) Brouillet, Urbatsch & Roberts.

2. Eurybia glauca (Nutt.) Nesom, Phytologia 77:260. 1994. *Eucephalus glaucus* Nutt.; *Herrickia glauca* (Nutt.) Brouillet; *Aster glaucus* (Nutt.) Torrey & A. Gray 1841 (non Nees 1818); *Aster glaucodes* Blake.

3. Eurybia horrida (Woot. & Standl.) Nesom, Phytologia 77:260. 1994. *Herrickia horrida* Woot. & Standl.; *Aster horridus* (Woot. & Standl.) Blake.

4. Eurybia kingii (D.C. Eaton) G.L. Nesom, comb. nov. Basionym: *Aster kingii* D.C. Eaton in S. Watson, Botany (Fortieth Parallel) 141, plate 16, figs. 1–6. 1871. *Machaeranthera kingii* (D.C. Eaton) Cronq. & Keck; *Tonestus kingii* (D.C. Eaton) Nesom; *Herrickia kingii* (D.C. Eaton) Brouillet, Urbatsch & Roberts.

4a. Eurybia kingii (D.C. Eaton) G.L. Nesom var. **barnebyana** (Welsh & Goodrich) G.L. Nesom, comb. nov. Basionym: *Machaeranthera kingii* var. *barnebyana* Welsh & Goodrich, Brittonia 33:299, fig. 5. 1981. *Aster kingii* var. *barnebyana* (Welsh & Goodrich) Welsh; *Tonestus kingii* var. *barnebyana* (Welsh & Goodrich) Nesom; *Herrickia kingii* var. *barnebyana* (Welsh & Goodrich) Brouillet, Urbatsch & Roberts.

4b. Eurybia kingii (D.C. Eaton) G.L. Nesom var. **kingii**

5. Eurybia pulchra (Blake) Nesom, Phytologia 77:261. 1994. *Aster glaucodes* subsp. *pulcher* Blake; *Aster glaucodes* var. *pulcher* (Blake) Blake; *Aster wasatchensis* var. *pulcher* (Blake) Welsh; *Eurybia glauca* var. *pulchra* (Blake) Brouillet; *Herrickia glauca* var. *pulchra* (Blake) Brouillet.

6. Eurybia wasatchensis (M.E. Jones) Nesom, Phytologia 77:262. 1994. *Aster glaucus* var. *wasatchensis* M.E. Jones; *Aster wasatchensis* (M.E. Jones) Blake; *Eucephalus wasatchensis* (M.E. Jones) Rydb.; *Herrickia wasatchensis* (M.E. Jones) Brouillet.

CONCLUSION

While the overall understanding of the herrickioid group is essentially the same as that of Brouillet et al.

(2004) and Brouillet (2006), the taxonomic alternative proposed here conveys an equally or more useful picture of the evolutionary standing of these species. Treating them within *Eurybia*, while explicitly pointing out evolutionary relationships suggested by the cladistic hypothesis, emphasizes their morphological similarity and geographic coherence. The Brouillet et al. taxonomy emphasizes the evolutionary discreteness of species that are morphologically inseparable by characters used elsewhere in the tribe and family to distinguish genera. The formal recognition of a paraphyletic group at generic rank, compared to the cladistically-derived alternative, has merit in this extreme example where morphology plays essentially no role at all in the classification. Further research may resolve the issue with less ambiguity.

ACKNOWLEDGEMENTS

I am grateful for loans from ASC and SJC, assistance of staff during study at BRIT, MO, and TEX-LL, specimen data from NMC for *Eurybia horrida*, and comments on the manuscript from John Pruski and three anonymous reviewers.

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BOOK REVIEW

Thomas G. Barnes, Deborah White, and Marc Evans. 2008. **Rare Wildflowers of Kentucky.** (ISBN 978-0-8131-2496-4; hbk.). The University Press of Kentucky, 663 South Limestone, Lexington, Kentucky 40508-4008, U.S.A. (**Orders:** www.kentuckypress.com, Hopkins Fulfillment Service, P.O. Box 50370, Baltimore, Maryland 21211-4370, 1-800-537-5487, 410-516-6998 fax). $39.95, 220 pp., 220 full-color photographs, 10" × 8 1/2".

Kentucky is gradually losing many plant species to housing and industrial development, including coal and timber removal. These activities have altered landscapes and resulted in the loss of native plant species, hence the focus of this book is on the conservation of rare wildflowers. The Introduction paints a dire scenario for the Kentucky flora with 273 plants in the state listed as endangered or threatened, an additional 52 of special concern, and 60 species (historic) have not been seen in 20 or more years. The color images were taken with film before the transition to digital cameras. Common names are used in the captions for the color floral images but the scientific names are in a special section at the end of the text. Photographs were by Thomas G. Barnes, a naturalist and award winning-photographer.

The first sections of the book are divided into a discussion of native species: Reasons for Decline of Native Species, Reasons for Protecting Native Plants, Natural Communities of Kentucky (includes a map that shows the Natural Regions of the state), Rarity, and Extinction and the Preservation of Species. This section is required reading for anyone who cares about the preservation of our native floras. An all too familiar theme is documented: human lifestyles and overpopulation (houses and cars) result in Habitat Loss, Invasive Exotic Species, Pollution, and Overcollection. There is a thoughtful and compelling discourse on reasons for protecting native plants. Natural communities are described and represented by landscape and habitat color images.

The section on The Rare Plants is divided into Forests (pages 49–96), Prairies and Glades (97–121), In and along Rivers (123–131), Wetlands (133–160), and Cliff Lines and Rockhouses (161–166). The flower images are sized to fill a full-page or half-page and are seen against usually a dark or black background.

Lists of plant names (both common and scientific binomials) as well as rare and extirpated plants identified with codes (E=endangered, T=threatened, S=special concern, H=historic, extirpated or extinct) that also include mosses and one lichen are included. A list of References and index follows.

The size and weight of the book will limit use in the field. The intent here is not to identify each plant to species, but in many cases the picture is distinct enough to serve as a picture guide. The threatened biodiversity, esthetic beauty of flowers, and the appeal for more conservation efforts to save habitats and larger tracts of land for future Kentuckians make this book a valuable contribution to the state flora of Kentucky.—*Harold W. Keller, Ph.D., Research Associate, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

THE PHYLOGENY OF *SELENIA* (BRASSICACEAE) INFERRED FROM CHLOROPLAST AND NUCLEAR SEQUENCE DATA

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ABSTRACT

Selenia Nutt. (Brassicaceae) is a North American genus of five species distributed from the central and southwestern U.S.A. to northern Mexico. While the basic taxonomy of this group has been well established, very little is known about the biology of individual species or the phylogenetic relationships among them. In this study, DNA sequence variation from the nuclear internal transcribed spacer and four non-coding chloroplast regions (the *trnL* intron; and the *petA-psbJ*, *trnQ–rps16*, and *trnS*^{GCU}-*trnG*^{UUC} intergenic spacers) was used to reconstruct the generic phylogeny. Results of parsimony and Bayesian analyses strongly supported the monophyly of both the genus and each individual species, and a completely resolved intra-generic phylogeny. The single instance of conflict between the nuclear and chloroplast topologies indicated historical hybridization between *Selenia grandis* and *Selenia mexicana*. The phylogenetic distinctiveness of *S. mexicana*, known only from a few collections in Nuevo León, combined with the relative lack of collections from Mexico suggested that additional diversity awaits discovery in this group.

RESUMEN

Selenia Nutt. (Brassicaceae) es un género norteamericano con cinco especies que se distribuyen desde el centro y sudoeste de Estados Unidos hasta el norte de México. Aunque la taxonomía básica de este grupo está bien establecida, se sabe muy poco sobre la biología de las especies o las relaciones filogenéticas entre ellas. En este estudio para la reconstrucción de la filogenia del género se emplearon cambios en las secuencias del espaciador de transcripción interna específico del ADN ribosomal (ADNr) y cuatro regiones no codificantes del ADN plastidial (el intrón trnL y los espaciadores intergénicos petA-psbJ, trnQ-rps16, y *trnS*^{GCU}-*trnG*^{UUC}). Los análisis de máxima parsimonia y bayesianos apoyan sólidamente la monofilia tanto del género, como de cada especie por separado, en una filogenia intragenérica completamente resuelta. El conflicto entre las topologías obtenidas con ADN nuclear y cloroplástico indican hibridación histórica entre *Selenia grandis* y *Selenia mexicana*. La distinción filogenética de *S. mexicana*, apenas conocida de unas pocas localidades en Nuevo León, junto con las pocas colecciones mexicanas sugiere que se espera descubrir más diversidad en este grupo.

INTRODUCTION

Selenia Nutt. (Brassicaceae) is a distinctive genus of five species distributed from the central and southwestern U.S.A. to northern Mexico (Fig. 1). *Selenia* species are small (<50 cm tall), spring flowering, herbaceous annuals found on a wide range of often seasonally wet habitats from sandstone glades (*S. aurea* Nutt.) to limestone hills (*S. dissecta* Torr. & A. Gray) to alluvial soils (*S. grandis* R.F. Martin) (Rollins 1993). *Selenia* can be easily distinguished from all other genera of the tribe Cardamineae by a combination of an annual habit, fully bracteate inflorescences, yellow flowers, silicles with distinct style, and biseriate, broadly winged seeds. Although *S. aurea* and *S. dissecta* can be found in multiple states, known from 57 and 14 counties, respectively, *S. grandis* and *S. jonesii* Cory are endemic respectively to southern and western Texas in the U.S.A. *Selenia mexicana* Standl. is known only from the Mexican states of Coahuila and Nuevo León, although the individual ranges of this species and of *S. dissecta*, *S. jonesii*, and *S. grandis* will surely expand following additional fieldwork in northern Mexico. This biogeographic uncertainty is representative of a basic lack of knowledge regarding *Selenia*, and little to no information exists concerning the reproductive biology, ecology, and phylogenetic relationships within this distinctive group (Al-Shehbaz 1988).

Although both morphological and biogeographic patterns within *Selenia* suggest certain null phylogenetic hypotheses, no study has addressed these evolutionary relationships. *Selenia aurea* is morphologically divergent from its congeners, with unappendaged sepals, pinnate (vs. bipinnate) leaves, and relatively long (>5 mm) styles. These features and its disjunct range (Fig. 1) suggest an isolated phylogenetic position for

J. Bot. Res. Inst. Texas 3(1): 169 – 176. 2009

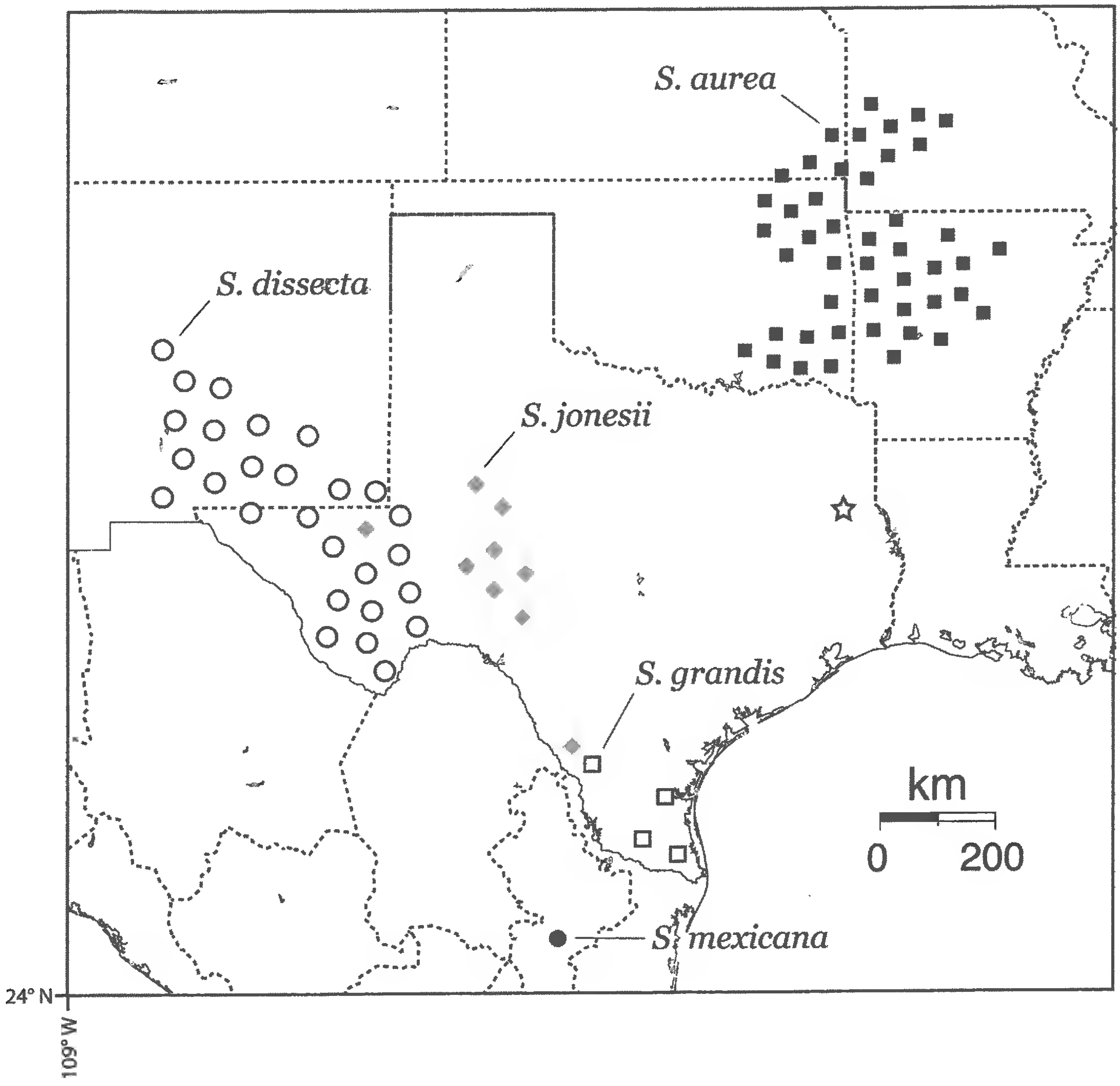

Fig. 1. The geographic distribution of *Selenia* species. All ranges are generalized and approximate, particularly that of *S. mexicana*. The potential range of *S. aperta* (see text) is noted with a star. The base map was created using software available at: http://www.aquarius.geomar.de/omc/make_map.html

this species. Within the remaining species, several characters, including possession of a horn-like (vs. pouch-like) sepal appendage and relatively long (>8 mm) sepals and anthers (>2.5 mm) suggest that *S. dissecta*, *S. grandis*, and *S. mexicana* form a natural group. These patterns of shared character variation, the morphological cohesiveness of individual species (Al-Shehbaz 1988), and the small size of the genus suggest that reconstructing the evolutionary relationships within this distinctive North American taxon will be tractable. This study aims to resolve the phylogenetic relationships between the five recognized species of *Selenia* using both chloroplast and nuclear DNA sequence variation.

MATERIALS AND METHODS

Taxon Sampling

Sample information appears in Appendix 1. Ten *Selenia* samples were analyzed, including two samples from each of the five species recognized in perhaps the most focused examination of the genus (Martin 1940). Three taxa that have been recognized by certain authors were not included, *S. jonesii* var. *obovata* Rollins, *S.*

aperta (S. Watson) Small, and *S. oinosepala* Steyerm. The first taxon is known only from the type collection (Rollins 1993), and the distinguishing character state (obovate fruits) has been considered to be an artifact of pressing the inflated fruits (Al-Shehbaz in ms.). Martin (1940) provided a detailed discussion of the lack of distinctiveness of both *S. aperta* and *S. oinosepala*, although both taxa warrant additional study (see discussion). *Leavenworthia* Torr. has been shown to be sister to *Selenia*, and the monotypic genus *Planodes* Greene has been shown, along with *Barbarea* R. Br., to be sister to the *Selenia/Leavenworthia* clade (Beilstein et al. 2006). Two *Leavenworthia* samples [*L. uniflora* (Michx.) Britton and *L. alabamica* Rollins] and a *P. virginicum* (L.) Greene sample were therefore used as outgroups. Nine of ten *Selenia* samples were obtained from herbarium material, and collections made as early as 1958 (see Appendix 1) yielded successful amplifications and sequences.

Molecular Methods

Extractions were performed with either a Qiagen (Qiagen, Valencia, CA) DNeasy Plant Mini Kit or a Viogene (Viogene U.S.A., Sunnyvale, CA) extraction kit. The nuclear internal transcribed spacer (ITS) region was amplified using the primers "ITS 1" (White et al. 1990) and either "ITS 4" (White et al. 1990) or "ITS2-26S.4" (Rauscher 2002). The *trnL*^{UAA} intron was amplified using the primers "C" and "D" (Taberlet et al. 1991). A portion of the chloroplast *trnS*^{GCU}-*trnG*^{UUC} intergenic spacer was amplified with the primers "1F" and "1R" (Säll et al. 2003). A portion of the chloroplast *petA-psbJ* intergenic spacer was amplified with the primers "5F" and "5R" (Säll et al. 2003). A portion of the chloroplast *trnQ*^{UUG}–*rps16* intergenic spacer was amplified with the primers "trnQ^{UUG}" and "rpS16x1" (Shaw et al. 2007). All reactions were performed under standard conditions. Products were visualized and purified via agarose gel electrophoresis with a Viogene gel extraction kit. Products were dye-labeled using a Big Dye Terminator Kit (Applied Biosystems, Foster City, CA), and analyzed on either a MJ Research BaseStation (MJ Research, Waltham, MA) or an Applied Biosystems 3130xl Genetic Analyzer. All sequences have been deposited in the EMBL nucleotide sequence database (Appendix 1).

Phylogenetic Analyses

The ITS and combined chloroplast (*trnL*, *trnS-trnG*, *petA-psbJ*, and *trnQ–rps16*) datasets were analyzed separately. Sequences were manually aligned in Se-Al (Rambaut 2002) and the aligned matrix was exported as a NEXUS file. All insertion/deletion (indel) events, both autapomorphic and synapomorphic, were scored except in the case of nucleotide repeats resulting in more than two indel character states (which were viewed as likely homoplasious), or in regions of uncertain alignment. In the case of overlapping indel events, the "simple gap coding" method of Simmons and Ochoterena (2000) was used. All positions involved in indels, or situated in regions of uncertain alignment were deleted prior to analysis, and indel events were coded as additional 1/0 characters and added to the end of the NEXUS file. Positions exhibiting poor sequence or additivity (multiple peaks presumably due to the presence of divergent ITS sequences in a single individual) were coded as ambiguous. For each dataset a heuristic maximum parsimony search with 100 random addition replicates was performed using PAUP* 4.0b10 (Swofford 2002) with the following parameters: starting trees obtained by stepwise addition, TBR branch swapping, "MulTrees" turned on, and steepest descent not in effect. Ten thousand bootstrap replicates were conducted with PAUP* 4.0b10 in order to obtain bootstrap support (BS). The best-fitting model of sequence evolution for each DNA region (indels and poorly aligned regions excluded) was identified using the Akaike Information Criterion in Modeltest 3.06 (Posada & Crandall 1998), and a Bayesian Markov Chain Monte Carlo analysis was performed on each dataset in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001). The combined chloroplast data were analyzed as a partitioned dataset, with the best-fitting model of sequence evolution for each separate region assigned to the corresponding partition (see Table 1). For both the ITS and combined chloroplast analyses, the indel characters were assigned the binary model of character evolution (Nst=1, Coding=Variable) as recommended in the MrBayes documentation. All Bayesian analyses comprised four independent runs, with four chains (one cold and three heated). Flat priors were used, with the exception of the rate prior that was set to allow rates to vary among partitions. Chains were run for 5 million generations, and trees were sampled every 1000 generations. Stationarity was evaluated by examining the standard deviation of split frequencies among runs and

Table 1. Relative phylogenetic information and model of sequence evolution chosen in each of the five DNA regions analyzed. [a]includes one inversion event. [b]Only a subset of the models evaluated by Modeltest are available for implementation in MrBayes.

Sequence characteristic	ITS	trnL	petA-psbJ	trnS-trnG	trnQ-rps16
Aligned length (bp)	520	578	397	301	523
Analyzed characters, including indels	516	493	327	286	470
Variable characters, including indels (%)	107 (21%)	23 (5%)	31 (9%)	13 (5%)	35 (7%)
Parsimony informative characters, including indels (%)	92 (18%)	9 (2%)	8 (2%)	3 (1%)	12 (3%)
Number of indels (parsimony informative)	3 (2)	7 (4)	8 (3)	3 (0)	9[a] (4[a])
substitution model selected by Modeltest	TVMef+I	K81uf+I	K81uf	K81uf+I	K81uf
substitution model implemented in MrBayes[b]	GTR+I	GTR+I	GTR	GTR+I	GTR

by plotting the log likelihood values from each run using Tracer 1.4 (Rambaut & Drummond 2007). These diagnostics indicated that runs reached stationarity quickly (within 100,000 generations) and I conservatively excluded the first 500,000 generations before obtaining a consensus phylogeny and clade posterior probabilities (PP).

RESULTS

Details regarding the length, variability, and model of sequence evolution chosen for each gene region are presented in Table 1. The analyzed ITS matrix of 516 characters yielded 107 (21%) variable and 92 (18%) parsimony-informative characters. The matrix contained 10 (0.1%) cells coded as either missing or ambiguous. Additivity, indicated by multiple peaks at a single nucleotide position, was limited to three samples. Two samples (*S. aurea* sample 1 and *S. mexicana* sample 2) exhibited multiple peaks at one position each, while *S. jonesii* sample 2 exhibited multiple peaks at four positions. At each of these four *S. jonesii* positions one of the two inferred nucleotides matched that from the other *S. jonesii* sample, with the other nucleotide a symplesiomorphy, typically observed in several congeners and the outgroup. Two of the three insertion/deletion events were parsimony-informative. Each of the 100 random addition replicate parsimony searches using the ITS dataset recovered the same island of five most parsimonious trees (MPTs) (length = 141, consistency index = 0.86, retention index = 0.91). One of the five MPTs, along with bootstrap percentages and Bayesian posterior probabilities, is shown in Figure 2a. The ITS data provided low support for the monophyly of *Selenia* (0.60 PP, 38% BS), but strong support (1.0 PP, 100% BS) for a "core *Selenia*" clade comprising *S. jonesii*, *S. grandis*, *S. dissecta*, and *S. mexicana*. The ITS data also provided strong support (0.97–1.0 PP) for the sister relationship of each pair of conspecific samples. Certain chloroplast regions failed to amplify in four samples (the *trnQ*^{UUG}–*rps16* intergenic spacer in *S. aurea* sample 2, *S. mexicana* sample 2, and the *L. alabamica* sample and the *trnS*^{GCU}-*trnG*^{UUC} intergenic spacer in *S. dissecta* sample 2). These samples were excluded from the combined chloroplast analysis. The analyzed chloroplast matrix of 1576 characters yielded 102 (6%) variable and 32 (2%) parsimony-informative characters. The chloroplast data matrix contained 29 (0.2%) cells coded as either missing or ambiguous. Eleven of the 27 insertion/deletion events were parsimony-informative. Each of the 100 random addition replicate parsimony searches using the combined chloroplast dataset recovered the same MPT (length = 112, CI = 0.95, RI = 0.88). The MPT, along with bootstrap percentages and Bayesian posterior probabilities, is shown in Figure 2b. Unlike the ITS data, which provided minimal support for the monophyly of *Selenia*, the combined chloroplast dataset strongly indicated such a relationship (1.0 PP, 99% BS). Strong support was also provided for the monophyly of "core *Selenia*" (1.0 PP, 100% BS), and two additional clades nested within this group. Although the four-locus chloroplast dataset was only able to assess the sister relationships of each pair of *S. jonesii* (1.0 PP, 100% BS) and *S. grandis* (1.0 PP, 95% BS) samples, a dataset including only *trnL* intron and *petA-psbJ* intergenic spacer sequences for all 10 *Selenia* samples provided strong support for the sister relationship of each pair of conspecific samples:

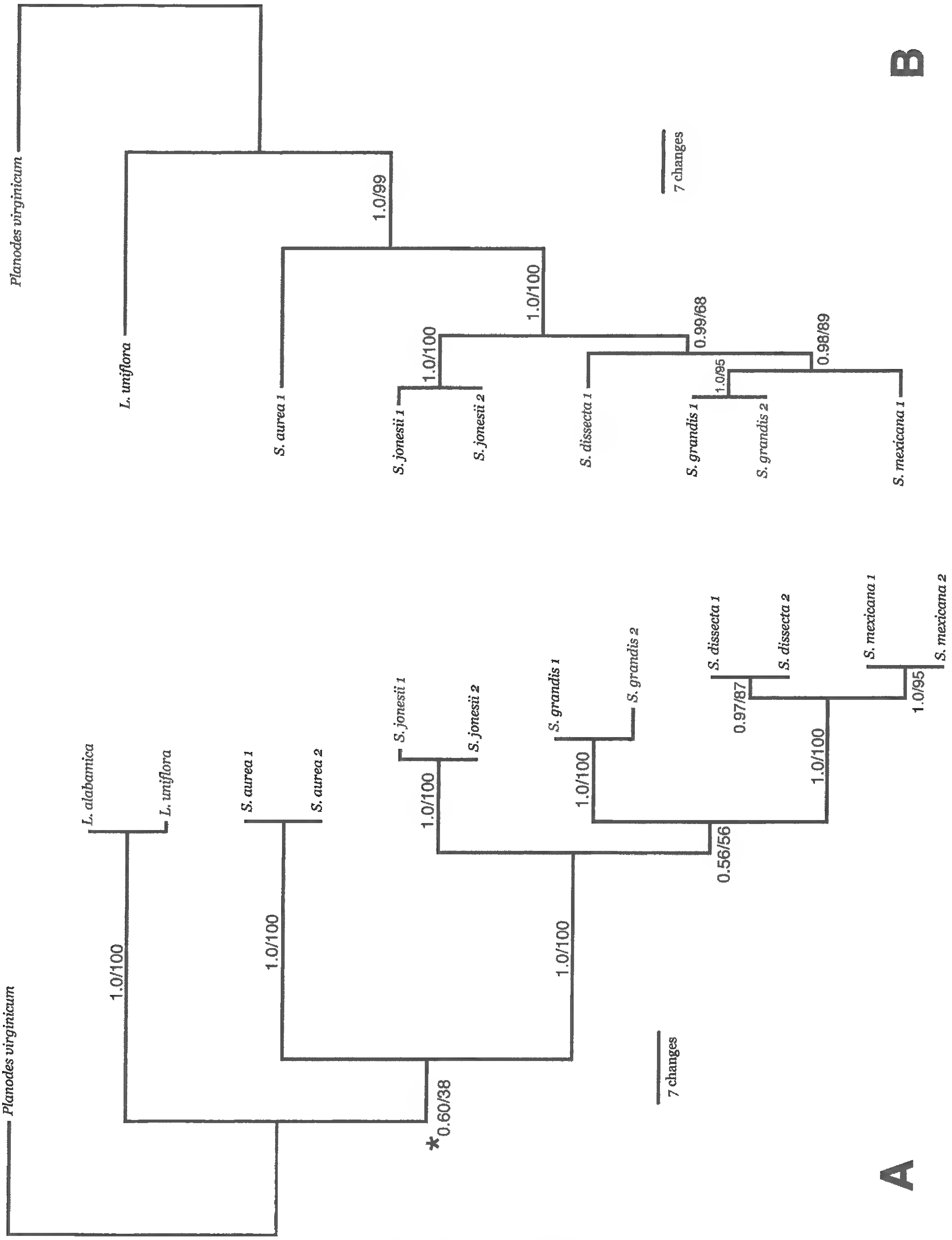

FIG. 2. A. One of five MPTs resulting from analysis of the ITS dataset. B. The single MPT resulting from analysis of the four-region chloroplast dataset (*trnL* intron; *trnQ–rps16*, $trnS^{GCU}$-$trnG^{UUC}$, and *petA-psbJ* intergenic spacers). Support values appear at each node (Bayesian posterior probabilities/bootstrap percentage). The node marked with an asterisk collapses in the ITS strict consensus tree. The trees were drawn using FigTree 1.1 (Rambaut 2008).

S. aurea (1.0 PP, 100% BS), *S. dissecta* (1.0 PP, 90% BS), and *S. mexicana* (1.0 PP, 86% BS). The only conflict between the chloroplast and nuclear topologies involved the placement of *S. mexicana*, which was sister to *S. dissecta* in the nuclear topology and sister to *S. grandis* in the chloroplast topology.

DISCUSSION

Selenia phylogeny

In general the nuclear and chloroplast datasets provide well-resolved and strongly supported phylogenetic reconstructions that are not only congruent with each other (Fig. 2), but with patterns of shared morphological character states. The core *Selenia* clade comprising *S. jonesii*, *S. grandis*, *S. dissecta*, and *S. mexicana* is distinguished by sepals bearing a dorsal appendage, bipinnate (vs. pinnate) leaves, and relatively short (<6 mm) styles. A more exclusive clade comprising *S. grandis*, *S. dissecta*, and *S. mexicana* is distinguished by possession of a horn-like (vs. pouch-like in *S. jonesii*) sepal appendage and relatively long (>8 mm) sepals and anthers (>2.5 mm). Interestingly, even though the *Selenia* key of Martin (1940) is artificial and therefore doesn't necessarily imply relatedness, if it is viewed as a bifurcating tree it perfectly matches the ITS topology presented in Figure 2a. The data clearly support the recognition of *S. mexicana* as distinct from *S. dissecta* (see below), suggesting that additional diversity is yet to be documented in this group. The three taxa not analyzed in this study (*S. jonesii* var. *obovata*, *S. aperta*, *S. oinosepala*) should therefore be subject to future molecular and morphological evaluation. *Selenia aperta* is a particularly intriguing case. This taxon was originally described as a variety of *S. aurea* by Watson (1895) based on material from San Augustine County, Texas, which exhibited broadly inflated silicles, a reduced septum, and a relatively long style. The variety was later given species status by Small (1903). Martin (1940) failed to locate the type material but examined both potential types and other specimens exhibiting these character states. He observed the variation described by Watson but found both variation among individuals from a single collection and no specimens that exhibited the full complement of characters. This variation, the potential disjunct range of *S. aperta* (noted in Fig. 1), and the chromosome number variation noted by Rollins and Rüdenberg (1977) all suggest that additional lineages remain to be identified within *S. aurea*.

Potential Hybridization and Chloroplast Capture

The only incongruence between the two topologies is the placement of *S. mexicana*, and morphological and biogeographical evidence suggest that the nuclear placement (as sister to *S. dissecta*) is correct and that the anomalous placement of *S. mexicana* by the chloroplast data is due to historical hybridization between *S. mexicana* and *S. grandis* followed by chloroplast capture. Chloroplast capture has been well documented empirically (Rieseberg & Soltis 1991), and appears to be possible under a range of biologically realistic situations (Tsitrone et al. 2003; Chan & Levin 2005). From a morphological standpoint, *S. dissecta* and *S. mexicana* are difficult to distinguish, with the latter exhibiting shorter (<2.5 vs. >3.5 mm) styles and spongy (vs. winged) seed margins, and recent workers (Al-Shehbaz 1988; Rollins 1993) have considered it a synonym of *S. dissecta*. Although the ranges of most *Selenia* taxa are poorly known, the existing biogeographic data also lend support to the proposed hybridization scenario, as known populations of *S. mexicana* are approximately 250 km closer to known populations of *S. grandis* than they are to populations of *S. dissecta* (Fig. 1). This evidence notwithstanding, *S. mexicana* is by far the most poorly known *Selenia* species, and additional cytological, genetic, and field studies are needed to thoroughly test this hypothesized gene flow. *Selenia dissecta* has been reported to be $2n = 14$, while *S. grandis* is known to be $2n = 24$ (Warwick & Al-Shehbaz 2006). The currently unknown chromosome number of *S. mexicana* will therefore reveal if the proposed hybridization event was via a polyploid or homoploid pathway. Evidence of additivity in the *S. grandis* or *S. mexicana* ITS sequences was limited to a single position in *S. mexicana* sample 2, indicating that any heterospecific ITS repeats have been largely eliminated due to backcrossing to conspecifics (the homoploid scenario) or concerted evolution (Franzke & Mummenhoff 1999). Particularly in a homoploid hybridization scenario, sequencing both individual cloned ITS sequences and other nuclear loci in an expanded sample set from across both species' ranges will reveal the extent of proposed introgression. Three individuals exhibiting

S. mexicana morphology (short styles in particular) were discovered in a recent survey of specimens from six major herbaria (BRIT, GH, MO, NY, TEX-LL, and US), all from within 100 km of the type locality of Galeana, Nuevo León (Standley 1937). Unfortunately, these collections contain few specimens from Mexico, and additional fieldwork is clearly needed. As noted in the introduction, the range of *S. mexicana* is but one of many aspects of *Selenia* species that are poorly documented. Future work, including expanded sampling of all proposed *Selenia* taxa, is therefore needed to understand the biology of this genus, information that can now be placed in an evolutionary context.

APPENDIX 1

Sample information. Taxon (sample number), voucher, year of collection (if herbarium material): country, state, county (if applicable), ITS EMBL, *trnL* EMBL, *trnS-trnG* EMBL, *petA-psbJ* EMBL, *trnQ-rps16* EMBL.

Leavenworthia alabamica **Rollins,** *Beck 486* **(MO)—U.S.A. Alabama. Franklin Co.: FM957596, FM957609, FM986404, FM986416, none**

Leavenworthia uniflora **(Michx.) Britton,** *Beck 516* **(MO)—U.S.A. Alabama. Morgan Co.: FM957595, FM957608, FM986403, FM986415, FM986429**

Planodes virginicum **(L.) Greene,** *Al-Shehbaz s.n.* **(MO)—U.S.A. Missouri: FM957594, FM957607, FM986402, FM986414, FM986428**

Selenia aurea **Nutt. (1),** *Beck 774* **(MO)—U.S.A. Missouri. St. Clair Co.: FM957598, FM957611, FM986406, FM986418, FM986427**

Selenia aurea **Nutt. (2),** *Stephens 29996* **(GH) 1969—U.S.A. Oklahoma. Nowata Co.: FM957597, FM957610, FM986405, FM986417, none**

Selenia dissecta **Torr. & A. Gray (1),** *Worthington 11630* **(NY) 1984—MEXICO. Chihuahua, FM957600, FM957613, FM986407, FM986420, FM986431**

Selenia dissecta **Torr. & A. Gray (2),** *Correll 38395* **(TEX-LL) 1970—U.S.A. Texas. Culberson Co.: FM957599, FM957612, none, FM986419, FM986430**

Selenia grandis **R.F. Martin (1),** *Turner 4323* **(TEX-LL) 1958—U.S.A. Texas. Nueces Co.: FM957603, FM957616, FM986410, FM986423, FM986435**

Selenia grandis **R.F. Martin (2),** *Correll 36762* **(TEX-LL) 1969—U.S.A. Texas. Hidalgo Co.: FM957604, FM957617, FM986411, FM986424, FM986434**

Selenia jonesii **Cory (1),** *Lundell & Lundell 16958* **(GH) 1961—U.S.A. Texas. Dawson Co.: FM957601, FM957614, FM986408, FM986421, FM986432**

Selenia jonesii **Cory (2),** *Mahler 8846* **(GH) 1981—U.S.A. Texas. Reagan Co.: FM957602, FM957615, FM986409, FM986422, FM986433**

Selenia mexicana **Standl. (1),** *Hinton 27036* **(TEX-LL) 1997—MEXICO. Nuevo León: FM957605, FM957618, FM986412, FM986425, FM986436**

Selenia mexicana **Standl. (2),** *Crutchfield & Johnston 5855* **(GH) 1960—MEXICO. Nuevo León: FM957606, FM957619, FM986413, FM986426, none**

ACKNOWLEDGMENTS

The author would like to thank the curators of BRIT, GH, MO, NY, TEX-LL, and US for herbarium loans. Special thanks go to Ihsan Al-Shehbaz for critical discussions, to George Yatskievych for help with locating *Selenia aurea*, to Eric Schuettpelz for help with Bayesian analyses, to Lisa Pokorny for providing the Spanish abstract, and to Ray Collier for laboratory assistance. Manuel B. Crespo (ABH) and two anonymous reviewers provided helpful comments on the manuscript. This study was funded by the Graduate Studies Program at the Missouri Botanical Garden and the Division of Biology and Biomedical Sciences at Washington University in St. Louis.

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PRELIMINARY INSIGHTS INTO THE PHYLOGENY AND SPECIATION OF *SCALESIA* (ASTERACEAE), GALÁPAGOS ISLANDS

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ABSTRACT

Scalesia Arn. (Asteraceae: Heliantheae) is a woody genus of fifteen species endemic to the Galápagos Islands. Morphological, distribution, and habitat data pertinent to speciation patterns in *Scalesia* were extracted from the literature and selected auxiliary specimens. All species of *Scalesia, Pappobolus* S.F. Blake, and *Simsia* Pers., along with selected species of *Viguiera* Kunth, were subjected to phylogenetic analysis (63 characters in 78 taxa). Homoplasy and incongruence among resulting trees prevented resolution of relationship and comparison of speciation events relative to its sister-group. Morphologically, species throughout these genera are marked primarily by homoplastic apomorphies. Based on broad characterization of habitats, morphological divergence (except for arborescence) and habitats appear to be poorly correlated. Sampling for future studies should be extended to include other groups in the derived Helianthinae.

RESUMEN

Scalesia Arn. (Asteraceae: Heliantheae) es un género leñoso de quince especies, endémico de las Islas Galápagos. Los datos morfológicos, de distribución y de hábitat relativos a los patrones de especiación en *Scalesia* se obtuvieron de la bibliografía y de especimenes auxiliares seleccionados. Todas las especies de *Scalesia, Pappobolus* S.F. Blake, y *Simsia* Pers., junto con algunas especies de *Viguiera* Kunth, fueron objeto de un análisis filogenético (63 caracteres en 78 taxa). La homoplasia e incongruencia entre los árboles resultantes impidió la resolución de parentesco y comparación de eventos de especiación relativa a su grupo hermano. Morfológicamente, las especies de estos géneros se distinguen primariamente por apomorfías homoplásticas. Basados en la amplia caracterización de los hábitats, la divergencia morfológica (excepto la arborescencia) y los hábitats parecen estar pobremente correlacionadas. El muestreo para futuros estudios debe ampliarse para incluir otros grupos de Helianthinae derivadas.

INTRODUCTION

Scalesia Arn. (Asteraceae: Heliantheae: Helianthinae) comprises fifteen species, all endemic to the Galápagos Islands. Howell (1941) accepted 18 species in four sections and related it to the Ecliptinae Lessing. Based on extensive field study, Eliasson (1974) recognized only 14 species, avoided the use of sections, discussed aspects of character evolution, and placed the genus in the Helianthinae Dumort. Hamann and Wium-Andersen (1986) described an additional species.

Recent studies on *Scalesia* have focused on intergeneric relationships (Schilling et al. 1994; Spring et al. 1999; Panero 2007), chemical diversity (Adsersen & Baerheim Svendsen 1986; Spring et al. 1997, 1999; Petersen et al. unpubl.), anatomy (Carlquist 1982), autecology (Itow 1995; Kitayama & Itow 1999; Hamann 2001), adaptive reproductive strategies (McMullen & Naranjo 1994; Nielsen et al. 2002, 2007), and population structure (Nielsen et al. 2003; Nielsen 2004). Chloroplast DNA restriction site analysis suggests that *Scalesia* belongs to a group of specialized genera, the "derived Helianthinae," that are embedded within a derived clade of *Viguiera* Kunth (Schilling et al. 1994). *Viguiera*, whose taxonomy has been unresolvable on morphological grounds, appears as a paraphyletic assemblage basal to all other genera in the Helianthinae on the basis of cpDNA restriction sites and internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA (Schilling & Jansen 1989; Schilling & Panero 2002). In an analysis in which *S. pedunculata* Hook.f. and several species of *Pappobolus* S.F. Blake were sampled (Schilling et al. 1994), *Scalesia* and *Pappobolus* were sister groups, and the next closest clade consisted of *Simsia* Pers. plus *Viguiera* ser. *Pinnatilobatae* S.F. Blake. However, the authors noted problems with interpretation of the three restriction sites synapomorphic for *Scalesia* and *Pappobolus* and concluded, "Thus, the relative relationships among *Scalesia*, *Pappobolus*, *Simsia*

and *Viguiera* ser. *Pinnatilobatae* are not well resolved by these data." Indeed, subsequent work has shown that chloroplast restriction sites, chloroplast genes, and ITS regions lack sufficient variation to resolve relationships in the derived Helianthinae (Schilling & Panero 1996, 2002; Petersen et al. unpubl.). However, recent analyses using external transcribed spacer (ETS) regions did find sufficient diversity to resolve species of *Helianthus* (Timme et al. 2007), a member of the derived Helianthinae, as well as species in other genera of the Heliantheae, such as *Montanoa* (Plovanich & Panero 2004).

Our interest is primarily in patterns of diversification, homoplasy, speciation rates, and degree of adaptation using *Scalesia* because it is the most speciose endemic angiosperm genus in the Galápagos. It is of interest that homoplasy among morphological characters of *Simsia* species prevented Spooner (1990) from publishing a cladistic analysis in his monograph. Likewise, Panero (1992) chose not to include phylogeny in his monograph of *Pappobolus,* instead recognizing only phenetic groupings. Thus, notable amounts of unanalyzed data are available in the literature for addressing the issue of homoplasy across *Scalesia* and relations. While it is our hope in the future to sample ETS regions in *Scalesia* species to determine their applicability in phylogenetic analysis, as well as use molecular phylogenies in investigating issues of interest to us, our goal here is to mine the existing pertinent morphological and ecological data that are available in the literature to provide a comparative context for later molecular studies. That is, we seek to provide insights into: **1)** sister-group and intrageneric relationships of *Scalesia,* **2)** homoplastic traits, **3)** relative amounts of speciation per clade, and **4)** directions for future molecular sampling. We anticipate that phylogenetic analysis of morphology may not yield consistent assessments of relationships or be congruent with molecular phylogenies (for example, see Plovanich and Panero [2004] concerning homoplasy in morphological taxonomic criteria in the Heliantheae). However, that result is not certain, for the hand-calculated Wagner parsimony networks of morphological data of *Dendroseris* and *Robinsonia* (Sanders et al. 1987), two other island endemics of the Asteraceae (Lactuceae and Senecioneae, respectively), did prove to be congruent with later molecular phylogenies (Crawford et al. 1992; Sang et al. 1995).

METHODS

Data.—Taxon sampling is based on the sister-group conclusions and Figure 1 of Schilling et al. (1994) and availability of supplemental specimens at the Botanical Research Institute of Texas and Bryan College. Morphological traits, coded as binary and multistate unordered characters, were extracted from published monographs of *Pappobolus* (Panero 1992), *Scalesia* (Eliasson 1974; Hamann & Wium-Andersen1986), *Simsia* (Spooner 1990), and species representing *Helianthus* L. (Schilling 2006), *Viguiera* sect. *Maculatae* (S.F. Blake) Panero & Schilling (Panero & Schilling 1988), and the outgroup *Bahiopsis* Kellogg (Schilling 1990). Selected dried specimens were consulted to verify codings obtained from the literature, supply missing data, and score representative species from *Viguiera* ser. *Grammatoglossae* S.F. Blake and ser. *Pinnatilobatae* (Table 1). Characters were chosen to maximize distinctions within *Scalesia, Pappobolus*, and *Simsia* and scored accordingly in the remaining taxa (Table 2), resulting in a number of characters being coded as polymorphisms. The compiled data constitute 63 characters in 78 species (Appendix).

Phylogenetic Analysis.—Parsimony analysis was conducted using PAUP* 4.0b10 (Swofford 1998). Heuristic searches were made with character optimization set to both accelerated and delayed transformation and with the following options: character weighting equal, 10 rounds of random addition sequence with 100 trees held at each addition, branch swapping by tree-bisection, MulTrees in effect, MaxTrees=100,000. Bootstrap analysis (10,000 replicates) was conducted using accelerated transformation by heuristic search with 10 trees held at each addition step. A final heuristic search, in which the majority-rule consensus tree from the bootstrap analysis was input for branch swapping only, was conducted using accelerated transformation with options as above. Based on the strict consensus tree from the first heuristic search, a reduced matrix of only the ancestral nodes of the outgroup, *Helianthus, Pappobolus, Simsia,* and *Viguiera grammatoglossa* + *V. stenophylla*; the remaining *Viguiera* species; and the species of *Scalesia* was generated. This matrix was subjected to a branch-and-bound search (options: accelerated transformation, equal weighting, MulTrees in effect, furthest addition sequence) and bootstrap analysis as above.

TABLE 1. Herbarium specimens consulted to supplement and verify data in literature. BRYAN is not yet officially recognized by Index Herbariorum but is used provisionally to designate the Henning Natural History Museum of Bryan College.

Taxon	Specimen	Locality	Herbarium
Bahiopsis			
B. deltoidea A. Gray	*S. White 5042*	Mexico: Baja, California. La Paz	SMU
B. parishii Greene	*Mahler & Thieret 5440*	USA: Arizona: Maricopa Co.: Sagauro Lake	SMU
Helianthus			
H. annuus L	*W. L. Henning* Acc. No. B 802	USA: Missouri: Boone Co.: W of Columbia	BRYAN
	G. Varga Acc. No. B 1794	USA: Tennessee: Rhea Co.	BRYAN
H. tuberosus L.	*W. L. Henning* Acc. No. B 804	USA: Missouri: Boone Co.: S of Columbia	BRYAN
Pappobolus			
P. acutifolius (S.F. Blake) Panero	*Panero & Galán 1399*	Perú: Ancash: Caráz	BRIT
P. matthewsii (Hochr.) Panero	*J. Panero 1353*	Perú: Amazonas: Pedro Ruiz	BRIT
P. robinsonii Panero	*Panero & Sánchez 1225*	Perú: Cajamarca: Celendin	BRIT
P. steubelii (Hieron.) Panero	*Panero et al. 932*	Perú: Cajamarca: Chalhuayaco	BRIT
Scalesia			
S. affinis Hook.f.	*Mears 5296*	Ecuador: Galápagos: Floreana	BRIT
S. helleri B.L. Rob.	*Mears 5494*	Ecuador: Galápagos: Santa Fe	BRIT
S. stewartii L. Riley	*Mears 5556*	Ecuador: Galápagos: Bartolomé	BRIT
S. villosa A. Stewart	*Mears 5226*	Ecuador: Galápagos: Gardner	BRIT
Simsia			
S. amplexicaulis (Cav.) Pers.	*A. Cronquist 9611*	Mexico: Michoacán: La Piedad	SMU
S. calva A. Gray	*J. Rodriguez 64*	Mexico: Nuevo León: Vallecillo	SMU
	U. Waterfall 16660	Mexico: Coahuila: Sabinas	SMU
S. eurylepsis S.F. Blake	*U. Waterfall 14300*	Mexico: San Luis Potosí: Ciudad de Valles	SMU
S. foetida (Cav.) S.F. Blake	*Yen & Estrada 6479*	Mexico: Chihuahua: Presa Chihuahua	BRIT
S. fruticulosa (Spreng.) S.F. Blake	*King & Guevara 5817*	Colombia: Cundinamarca. Chipaque	SMU
S. holwayi S.F. Blake	*R. M. King 7337a*	Guatemala: Alta Verapaz: San Cristóbal Verapaz	BRIT
S. sanguinea A. Gray	*C. G. Pringle 11513*	Mexico: Jalisco: Guadalajara	SMU
Viguiera ser. **Grammatoglossae**			
V. cordifolia A. Gray	*J. Cornelius 227*	USA: Texas: Brewster Co.: Black Gap WMA	SMU
	D. S. Correll 15006	USA: Texas: Jeff Davis Co.: Davis Mts.	SMU
V. grammatoglossa DC.	*J. Rzedowski 34497*	Mexico: Oaxaca. Chilapa de Díaz	VDB
Viguiera sect. **Maculatae**			
V. adenophylla S.F. Blake	*E. Estrada 1889*	Mexico: Nuevo León. Iturbide	BRIT
Viguiera ser. **Pinnatilobatae**			
V. stenoloba S.F. Blake	*A. Krings 288*	USA: Texas: Presidio Co.: Big Bend Ranch State Park	BRIT
	Nee & Diggs 25354	Mexico: Edo. Coahuila. Mun. San Pedro	BRIT
	A. Treverse 2215	USA: Texas: Brewster Co.: Big Bend National Park	BRIT

Bayesian analysis was conducted using MrBayes v3.1.2 (Huelsenbeck & Ronquist 2001) on both the full and the reduced matrices using the default settings of the standard discrete evolutionary model. Analysis of the full matrix was run for 200,000,000 generations and sampled once every 100,000 generations; the reduced matrix was run for 400,000 generations and sampled every 100 generations.

Habitat Characterization.—Geographic distributions and habitat features were estimated from Cronquist (1971), Eliasson (1976), Hamann and Wium-Andersen (1986), and personal observation of one of us (RWS).

TABLE 2. Characters and character states used in data matrix (Appendix). Character states are unordered.

1. **Habit** 0: shrub, 1: tree, 2: suffrutescent perennial, 3: perennial herb, 4: annual
2. **Hair type presence** 0: unspecialized pubescent, 1: villous to lanate, 2: scabrous or strigose
3. **Glandular trichomes** 0: absent, 1: present
4. **Twig pubescence color** 0: white to gray, 1: yellow or green
5. **Leaf phyllotaxy** 0: alternate, 1: opposite
6. **Leaf heterchrony** 0: inflorescence leaves ± size of cauline lvs., 1: lvs. partially or gradually reducing into inflor., 2: lvs. much reducing into inflor.
7. **Leaf outline** 0: ovate, 1: lanceolate, 2: cordate, 3: triangular, 4: elliptic, 5: linear-oblong
8. **Leaf margin lobing** 0: unlobed, 1: lobed 1/4 to midrib, 2: lobed 1/2 to midrib, 3: lobed 3/4 to midrib, 4: regularly deeply lobed nearly to midrib
9. **Leaf margin serration** 0: completely entire, 1: crenate or serrulate, indistinctly toothed, 2: distinctly serrate
10. **Leaf margin orientation** 0: flat, 1: revolute
11. **Leaf adaxially strigose** 0: not strigose, scabrous, or sericeous, 1: moderately strigose, scabrous, or sericeous, 2: densely strigose, scabrous, or sericeous
12. **Leaf abaxially strigose** 0: not strigose, scabrous, or sericeous, 1: moderately strigose, scabrous, or sericeous, 2: densely strigose, scabrous, or sericeous
13. **Leaf abaxially lanate** 0: not villous or lanate, 1: moderately villous or lanate, 2: densely villous or lanate
14. **Leaf surface reflectance, adaxially** 0: dull, 1: shiny
15. **Leaf texture** 0: herbaceous/chartaceous, 1: leathery, 2: thinly membranous
16. **Leaf venation** 0: triplinerved, 1: pinninerved
17. **Leaf midrib position adaxially** 0: level or above surface, 1: sunken below surface
18. **Petiole shape** 0: unwinged, 1: wing tapering in apex, 2: wing tapering above base, 3: wing broad to basal insertion, 4: winged at base only
19. **Petiole length** 0: 0–9 mm, 1: >10 mm
20. **Inflorescence reiteration** 0: monochasial, 1: dichasial
21. **Head arrangement** 0: more/less solitary, 1: open panicle, 2: tightly aggregate panicle
22. **Head size (w/o rays)** 0: very large >30 mm, 1: large 15–30 mm, 2: moderate 7–15 mm, 3: small <7 mm
23. **Involucre shape** 0: campanulate-subcylindric, 1: urceolate-hemispheric
24. **Phyllary series** 0: 3–4, 1: 2, 2: (4–)5–6
25. **Phyllary shape** 0: oblong to obtrullate, 1: narrowly elliptic, 2: lanceolate, 3: subulate-attenuate, 4: ovate
26. **Phyllary, outer series, shape** 0: not spatulate, 1: spatulate
27. **Phyllary size to florets** 0: subtending floresets, 1: overtopping florets
28. **Phyllary size ratio, outer/inner** 0: outer ± inner, 1: outer < 2/3 inner
29. **Phyllary color** 0: normal green, 1: stramineous ± with green stripes, 2: blackish green, 3: purple
30. **Phyllary consistency** 0: scale-like, 1: foliaceous
31. **Phyllary pubescence density** 0: revealing surface, 1: obscuring surface
32. **Phyllary margin, cilia** 0: without cilia, 1: ciliate
33. **Phyllary tip shape** 0: blunt or abruptly acute, 1: acuminate, long acute
34. **Phyllary tip orientation** 0: erect or appressed, 1: reflexed or spreading
35. **Phyllary base thickness** 0: unthickened, herbaceous, 1: base slightly thickened indurate, 2: base conspicuously thickened indurate
36. **Ray presence** 0: absent, 1: present in full complement, 2: present in part
37. **Ray orientation** 0: spreading, 1: strongly reflexed or recurved
38. **Ray ligule length** 0: <1.5 cm, 1: 1.5–3.0 cm, 2: > 3 cm
39. **Ray apex fusion** 0: shallowly 2-3 toothed, 1: deeply 2-3 notched/lobed, 2: irregularly, barely fused or lipped
40. **Ray ovary shape** 0: ovoid/lenticular/fusiform, 1: linear
41. **Palea length** 0: about equalling phyllaries, 1: protruding above phyllaries, 2: shorter than phyllaries
42. **Palea apex pubescence** 0: glabrous, 1: pubescent
43. **Palea segmentation** 0: lacking, 1: shallow, 2: deep
44. **Palea segments, shape** 0: elliptic, 1: triangular, 2: ovate-rounded, 3: subulate, 4: oblong-ligulate
45. **Palea segments, orientation** 0: erect, 1: diverging or reflexed, 2: strongly overlapping, 3: inflexed or hooded
46. **Palea segments, central one** 0: equal to laterals, 1: much longer than laterals
47. **Disk corolla color** 0: yellow to orange, 1: brown, 2: pale yellow, 3: white, 4: pink, 5: deep purple
48. **Disk corolla tube to throat length ratio** 0: ~3–4, 1: ~5–10, 2: ~1
49. **Disk corolla tube pubescence** 0: glabrous, 1: puberulent
50. **Disk corolla throat pubescence** 0: glabrous, 1: puberulent
51. **Disk corolla lobes abaxially** 0: without dark pigment, 1: with black pigment, 2: with purple pigment
52. **Anther color** 0: yellow, 1: black, 2: (yellow) purple distally, 3: maroon or brown
53. **Anther appendix color** 0: stramineous, 1: all or part black, 2: white
54. **Style branch color abaxially** 0: without black pigment, 1: with black pigment
55. **Style branch apex** 0: deltate, 1: attenuate
56. **Style branch appendage** 0: absent, 1: present
57. **Achene length** 0: < 3 mm, 1: 3–5 mm, 2: > 5 mm
58. **Achene pubescence** 0: glabrous, 1: sericeous
59. **Achene compression** 0: biconvex-lenticular, 1: laterally flat but slightly biconvex, 2: strongly lat. flattened, 3: terete or trigonous
60. **Pappus development** 0: absent, 1: callous ring only, 2: awns and/or scales
61. **Pappus, no. awns** 0: 0, 1: 1 (often small), 2: 2, 3: multiple
62. **Pappus, intervening scales** 0: absent, 1: present
63. **Pappus persistence** 0: persistent, 1: caducous

RESULTS

Sister-group relationships.—The first two heuristic searches (random-addition with accelerated vs. delayed character transformations) resulted in 100,000 shortest trees each (442 steps). These and their strict consensus trees were partially incongruent with the majority-rule tree of the bootstrap analysis. In the delayed transformation search, *Viguiera adenophylla* was sister to all other ingroup taxa, and *Pappobolus* was paraphyletic with *P. ecuadoriensis* sister to all remaining taxa. Of these, one clade contained *P. sagasteguii*, a subclade of *V. stenoloba* + *Scalesia*, and a subclade containing the remaining *Viguiera* species, *Helianthus*, and *Simsia* as monophyletic genera. The other clade contained all remaining species of *Pappobolus*. The accelerated transformation search resulted in *V. adenophylla* as above but the remaining ingroup taxa constituted five clades in an unresolved polytomy: *V. cordifolia, Helianthus, Scalesia, Simsia*, and one having a monophyletic *Pappobolus* sister to *V. grammatoglossa* + *V. stenoloba*.

The third heuristic search (bootstrap majority-rule tree input and branches swapped) resulted in all 100,000 trees being congruent with the bootstrap analysis, though one step longer (443) than the trees from the first two searches. In the strict consensus tree of this analysis (Fig. 1), the ingroup formed three major clades. A monophyletic *Pappobolus* was sister to the remaining ingroup taxa. Of these, one clade consisted of *V. adenophylla* and *Scalesia* as sister groups. The other clade contained a tetrachotomy: *Simsia, Helianthus, V. cordifolia*, and *V. grammatoglossa* + *V. stenoloba.*

The Bayesian majority-rule consensus tree (analysis final average standard deviation 0.0078) added yet another possible arrangement. Of the ingroup taxa, *Scalesia* + *V. adenophylla* were sister to the remainder, which formed a polytomy: *V. grammatoglossa, V. stenoloba*, nine species of *Pappobolus*, a clade with all the remaining *Pappobolus*, and a clade consisting of *V. cordifolia, Helianthus*, and *Simsia*.

In all of the consensus trees, *Simsia* was completely unresolved or nearly so, and *Pappobolus* contained two to three large sets of unresolved species. *Scalesia* was reasonably well resolved but its topology differed among trees. All heuristic searches found the arboreous species as a resolved clade (*S. cordata* A. Stewart, *S. microcephala* B.L. Rob., *S. peduculata* basal), the lobe-leaved species (*S. baurii* Robinson & Greenman, *S. helleri* Robinson, *S. incisa* Hook.f., *S. retroflexa* Hemsl.) as a partially or fully resolved clade, the three species with elongate phyllaries (*S. atractyloides* Arn., *S. stewartii* L. Riley, *S. villosa* A. Stewart basal) as a grade or clade, and a clade of *S. divisa* Andersson + *S. gordilloi* O.J. Hamann & Wium-And. In two searches the arboreous clade was sister to the remainder with the elongate-bracted clade deeply imbedded; in the third the elongate-bracted group was a basal grade with the arboreous clade deeply imbedded. In the Bayesian majority rule tree, *Scalesia* was an eight-way polytomy of the arboreous, elongate-bracted, and lobe-leaved clades, *S. affinis* Hook.f., *S. aspera* Andersson, *S. crockeri* J.T. Howell, *S. divisa*, and *S. gordilloi.*

Branch-and-bound analysis of the reduced matrix produced 13 trees of equal length (163 steps). In the strict consensus tree (Fig. 2), *V. adenophylla* was sister to the other ingroup taxa, which formed a tetrachotomy: *Scalesia, Helianthus, Simsia* + *V. cordifolia*, and *Pappobolus* + the *V. grammatoglossa-stenophylla* ancestor. In *Scalesia*, the arboreous clade (unresolved) was sister to the remainder which formed a polytomy of *S. affinis, S. aspera, S. crockeri, S. divisa, S. gordilloi*, a partially resolved clade of the lobe-leaved species, and a resolved elongate-bracted clade. However, the Bayesian majority rule tree (analysis final average standard deviation 0.0070) of the reduced matrix differed by being nearly identical to one of the most parsimonious branch-and-bound trees (Fig. 2) except that 1) the arboreous species formed a basal grade with *S. cordata* + *S. microcephala* sister to the remaining species, 2) there was no resolution among *S. affinis, S. aspera, S. crockeri* and the remaining clades, and 3) *S. retroflexa* was basal to the other members of the lobe-leaved clade.

Apomorphies and homoplasy.—In one of the 100,000 equally parsimonious trees from the third heuristic search the composite consistency index (CI) was 0.24 (excluding two uniformative characters), the rescaled CI (RC) was 0.17, and the retention index (RI) was 0.71. In this tree, the only synapomorphies of *Scalesia* with a consistency index over 0.4 were ray florets absent and anthers black. The only comparable synapomorphy for *Pappobolus* was anthers yellow and for *Simsia*, phyllaries not thickened at base and achenes strongly laterally flattened.

The composite CI of the branch-and-bound trees (Fig. 2) was 0.49 (including only 51 informative char-

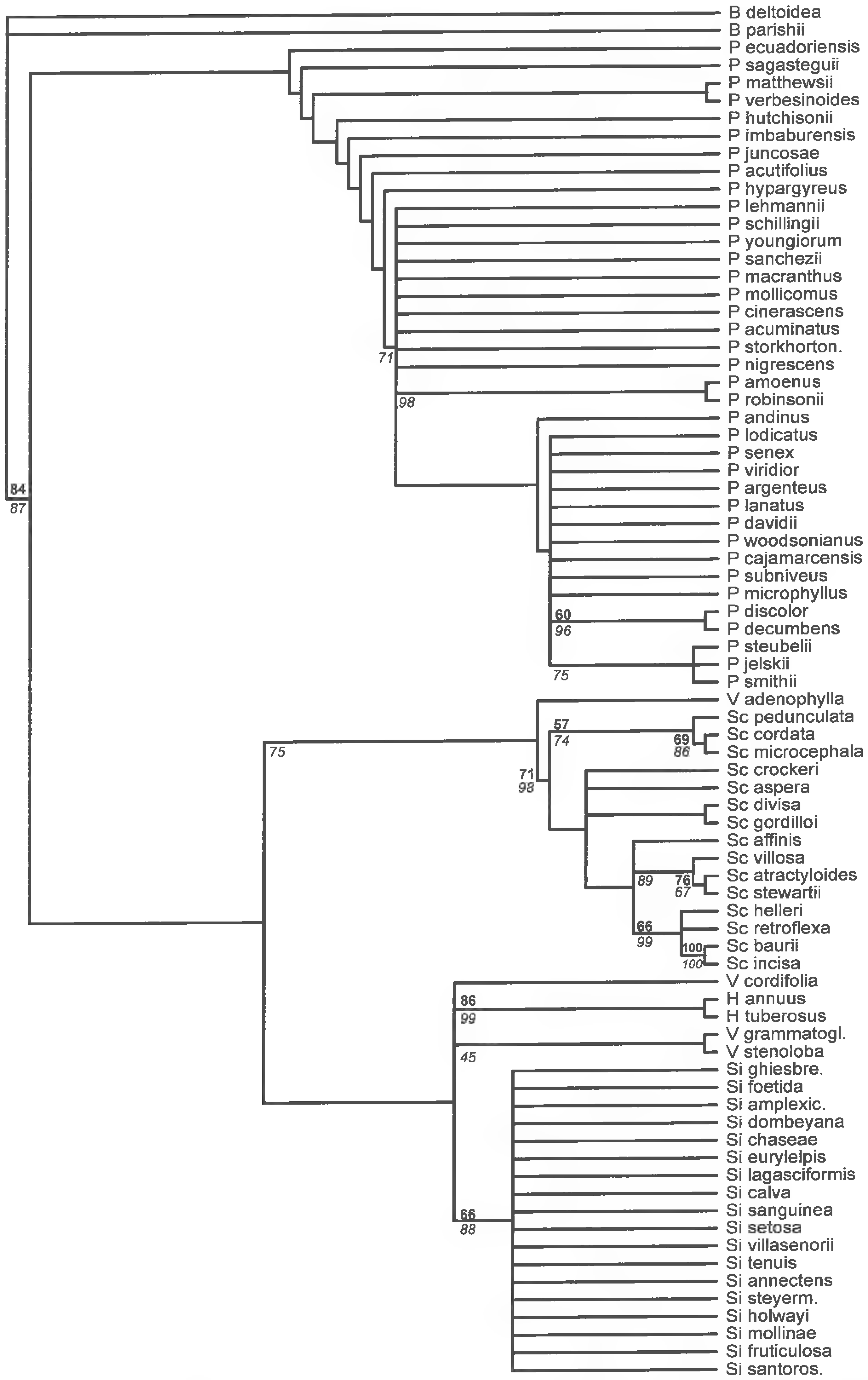

Fig. 1. Strict consensus tree of third heuristic search (branch-swapping of input bootstrap majority-rule tree) of full data matrix, based on 100,000 equally parsimonious trees. Bold numbers above branches indicate bootstrap values; italic numbers below branches indicate Bayesian posterior probabilities. Generic abbreviations: B=*Bahiopsis*, H=*Helianthus*, P=*Pappobolus*, Sc=*Scalesia*, Si=*Simsia*, V=*Viguiera*.

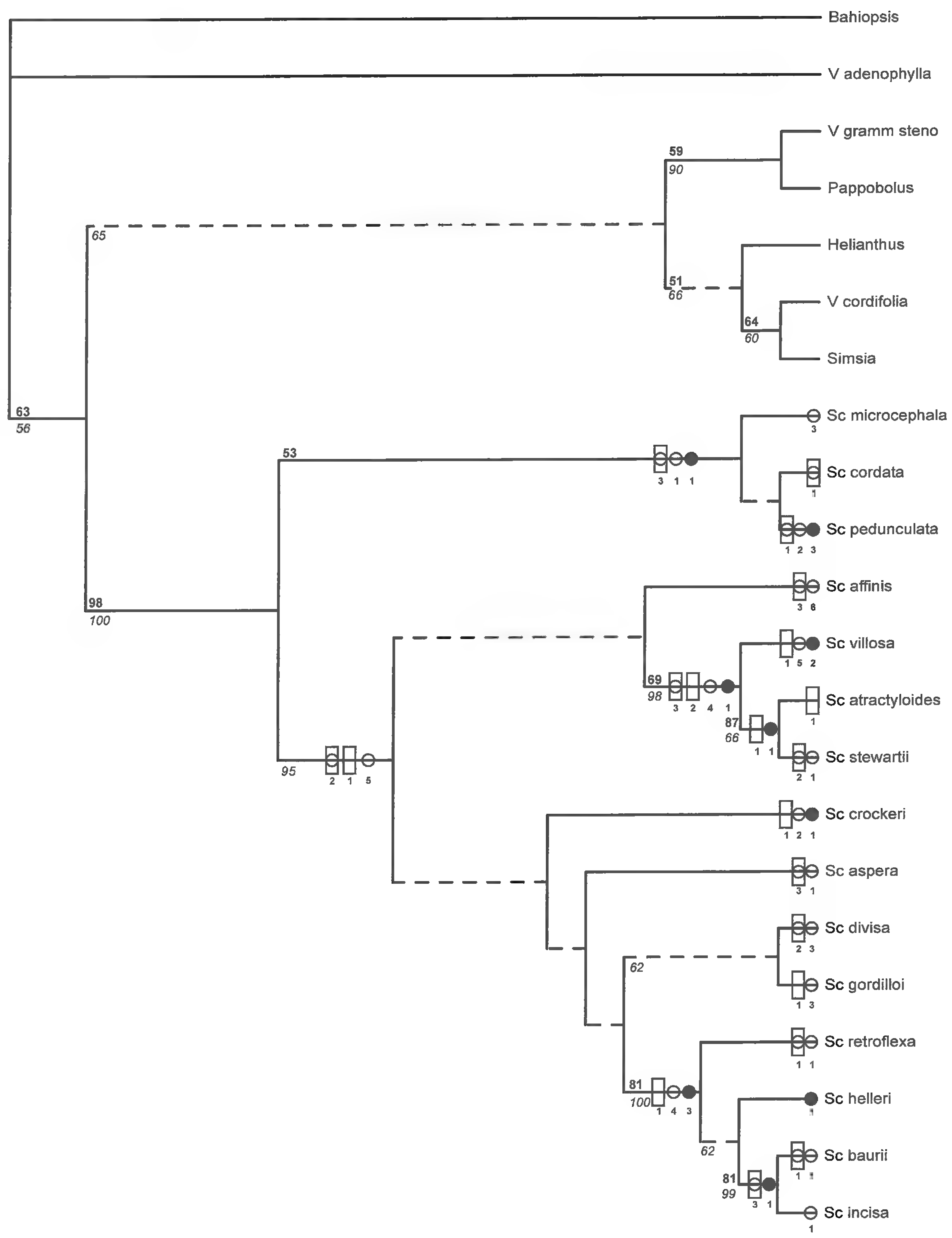

Fig. 2. One of 13 equally parsimonious trees obtained from branch-and-bound analysis of *Scalesia*. Bold numbers above branches indicate bootstrap values; italic numbers below branches indicate Bayesian posterior probabilities. Dashed lines indicate branches that are collapsed in the resulting strict consensus tree. Generic abbreviations are as in Figure 1. Numbers of apomorphies on branches of *Scalesia* by class as follows: **solid dot** = unique (synapomorphies/autapomorphies), **open circles** = homoplasy restricted to species of *Scalesia*, **box** = homoplastic between *Scalesia* and another genus, **box with circle** = homoplastic both within *Scalesia* and with external genus.

acters), the RI 0.66, and RC 0.37. In this tree, the synapomorphies for *Scalesia* supported by a consistency index of 0.4 or greater included: capitula 15-30 cm diameter; involucre hemispheric to urceolate; phyllaries oblong to obtrullate and erect/appressed; ray absent but, when present deeper within the clade, reflexed with irregularly fused lobes; paleae deeply segmented; corollas white; anther appendices white; and achenes glabrous. Black anthers, instead, appeared to be synapomorphic for the ingroup minus *V. adenophylla*.

The third heuristic search of the full matrix resulted in only six characters that were completely consistent: four involved autapomorphies (or synapomorphies for species pairs), whereas only three involved synapomorphies of significant clades. Eleven homoplastic characters had consistency indices of 0.5 or higher. Four of these (phyllary base thickening, ray presence, fusion of ray lobes, and shape of palea segments) were parallelisms or reversals within *Scalesia*; only two (growth habit, orientation of palea segments) were parallelisms between species of *Scalesia* and other genera. Forty-six characters had consistency indices lower than 0.5, of which 30 appeared in both *Scalesia* and other genera, 15 in only other genera, and only one (ratio of corolla tube to limb lengths) just in *Scalesia*.

The branch-and-bound matrix had only 55 variant characters. Sixteen were consistent, and, of these, eleven involved synapomorphies of significant clades. Twenty-five characters were homoplastic with a consistency index of 0.5 or higher including nine appearing within *Scalesia* and six in *Scalesia* and related genera. Only 14 characters were below the 0.5 consistency index level with only one restricted to species of *Scalesia* (as above), only one outside of *Scalesia*, and the remaining 12 appearing in both *Scalesia* and other genera.

Geographic distributions and ecology.—All species except *Scalesia affinis*, which is sympatric with *S. aspera, S. crockeri, S. helleri, S. retroflexa*, and *S. villosa*, are narrowly allopatric or parapatric (Fig. 3). Some have disjunct populations occurring on separate islands. All the arboreous species (*S. pedunculata, S. cordata*, and *S. microcephala*) are found in the moist forest zone in mid to upper elevation and are geographically isolated from each other. *Scalesia affinis*, the only species with consistently radiate capitula, has the widest distribution and occupies the widest range of habitats; occurring most commonly in the arid zone, it ranges from coastal to lower parts of the moist forest zone. All remaining species are found in the low elevation (littoral, arid, and dry forest zones) (Table 2). Due to overlap of preferences, there appears to be little habitat differentiation among these species. Only the rare species *S. crockeri* and *S. retroflexa* are known only from littoral sites. Other species (e.g., *S. atractyloides*; Mauchamp et al. 1998) are restricted to cliffs due to grazing by feral goats but historically ranged over more littoral and arid sites.

DISCUSSION

Phylogenetic relationships.—The present results support the monophyly of *Scalesia, Simsia*, and *Helianthus*. Although molecular data (Schillling et al. 1994) support *Pappobolus* as monophyletic, the present data are equivocal in that regard, in some cases placing *Scalesia, Simsia, Helianthus*, and associated *Viguiera* species within a paraphyletic *Pappobolus*.

Morphological data do not resolve the sister-group relationships of *Scalesia*, leaving open the possibility that *Scalesia* is sister to a group of *Viguiera* species or that *Scalesia* arose more or less simultaneously with *Simsia, Helianthus*, and *Pappobolus* (with any associated *Viguiera* species). As *Viguiera* sect. *Maculatae* is basal among the derived Helianthinae based on DNA restriction site and ITS data (Schilling & Jansen 1989; Schilling et al. 1994; Schilling & Panero, 1994, 1996, 2002), the sister-group placement of *Scalesia* and *V. adenophylla* in some results is due possibly to experimental error in coding or identification. Furthermore, Schilling and Panero's (1996) molecular analysis suggests that *Tithonia* Desf. ex Gmelin, *Viguiera* subg. *Amphilepis* S.F.Blake, and *V.* sect. *Paradosa* S.F.Blake are closer to *Pappobolus* than is *Simsia* and should be considered as potential sister groups of *Scalesia*.

Within *Scalesia* there is general support for the lobe-leaved, arboreous, elongate-bracted, and *divisa-gordilloi* clades. Because the arboreous clade did not receive support from a minority of analyses, it is interesting that Eliasson (1974) considered *S. pedunculata* to have developed arborescence convergently with *S. cordata* and *S. microcephala*. If all variant trees based on the various analyses preformed are considered, the only clades receiving total support are the lobe-leaved clade and a terminal clade of *S. atractyloides* and *S.*

FIG. 3. Distribution of *Scalesia* species, estimated from literature, including historically known ranges. Fine stippling = *Scalesia affinis*, course stippling = lobe-leaved clade; cross hatching = arboreous clade, vertical lines = elongate-bracted clade, solid dark gray = *divisa-gordilloi* clade; solid light gray = remaining species.

stewartii, more in line with Eliasson's conclusions. Within the lobe-leaved clade, there is total support for *S. baurii* and *S. incisa* as a clade, but only partial support for *S. helleri* + *S. retroflexa*. In this case, these clades and all remaining species would radiate from a basal polytomy. If, indeed, *Scalesia* is an example of radiation by the rapid dispersal of founder populations from an initial colonizer, an unresolved basal polytomy may portray more accurately the history of *Scalesia* than any of the less-supported but more-resolved trees.

Homoplasy.—Obviously, the degree of resolution of the particular cladogram examined will affect the level of homoplasy among taxa. Because the branch-and-bound analysis resulted in 13 equally parsimonious well-resolved trees and the comparison of all analyses suggest a minimally resolved polytomy within *Scalesia*, the level of homoplasy discussed is based on the branch-and-bound consensus tree, which is intermediate in resolution (Fig. 2). *Scalesia* itself is delimited by five synapomorphies and 11 homoplastic apomorphies (two among *Scalesia* species, five with external taxa, and four occurring both inside and outside *Scalesia*). Of the 15 species and 6 clades in *Scalesia*, only 9 are delimited by unique apomorphies. Of the 90 total character-states apomorphic for clades and species, 14 (16%) are unique, 42 (46%) are homoplastic only within *Scalesia*, 9 (10%) are homoplastic only between *Scalesia* and external taxa, and 25 (28%) are homoplastic between *Scalesia* taxa as well as with external taxa. It will be of interest to see the level of morphological homoplasy on DNA-sequence trees when these become available.

Table 3. Characterization of habitats of *Scalesia* species, estimated from the literature.

	Moist Forest Zone	Littoral Zone	Arid Zone	Dry Forest Zone	Volcanic Soil	Lava Gravel	Fissured Lava
cordata	x				x		
microcephala	x				x	x	
pedunculata	x				x	x	
affinis	x	x	x	x	x	x	x
villosa		x	x			x	x
atractyloides		x	x			?	x
stewartii		x	x			x	x
incisa		?	x			x	
baurii	?		x	x	?	x	
retroflexa		x				x	x
helleri		x	x			x	x
gordilloi		x	x	x		x	
divisa			x	x		x	x
aspera		x	x	x		x	x
crockeri		x				x	x

The characters that (at least some states of which) are not homoplastic in *Scalesia* include tree habit, leaf outline, leaf marginal lobing, dense villous hairs on abaxial leaf and phyllary surfaces, petiole shape, phyllary shape, ray orientation, palea segment shape and orientation, disk corolla color, disk corolla shape, anther appendage color, achene pubescence, and pappus development. However, all other characters and some states of the above are homoplastic. Some interesting examples include: 1) the presence of villous hairs in *S. villosa* and *Pappobolus*; 2) more or less solitary capitula of most species of *Scalesia* and *Viguiera grammatoglossa* and *V. stenoloba*; 3) multiple changes in size of capitula in *Scalesia*; 4) phyllary shape in *S. crockeri* and *Helianthus*; 5) palea length in *S. microcephala*, the elongate bracted clade, and *Pappobolus*; 6) glabrous paleae in *S. aspera, S. baurii, S. incisa, S. microcephala*, and *Pappobolus*; 7) length of the central lobe of the paleae in *S. affinis, S. crockeri, S. microcephala, S. villosa*; 8) disk corolla tube length in *S. affinis, S. baurii, S. stewartii*, the lobe-leaved clade, and *Viguiera adenophylla*; and 9) glabrous disk corolla tubes in *S. affinis, S. aspera, S. villosa*, the arboreous clade, and *Simsia*. Many of these characters are associated with the palea and corolla structure. According to Plovanich and Panero (2004), such characters associated with reproductive success should be convergent in the Heliantheae due to strong selection pressures. Whether this will be true in *Scalesia* remains to be investigated using molecular data sets.

In regard to the presence of rays in certain species of *Scalesia*, Eliasson (1974) concluded that rays were lost in the ancestor of *Scalesia*, regained as scattered bilabiate disk corollas in the lobed-leaved species, and regained as nearly typical rays in *S. affinis*. His hypothesis is supported by the results presented here. If the *affinis*-type rays are the end of a character transformation involving the bilabiate disk corollas or are a reversal to true rays, then this constitutes an additional homoplastic trait. Presumably rays increase insect pollination and should be selected for on islands as the insect fauna diversifies, as suggested by the wider distribution of *S. affinis*. However, the addition of artificial rays to *S. pedunculata* did not increase its fitness (Nielsen et al. 2002). Therefore it is not clear that this character has high adaptive value in *Scalesia*.

Despite the species and clades of *Scalesia* being delimited primarily by unique combinations of homoplastic character states as opposed to unique apomorphies, the species all appear to be distinct. Moreover, the full data set suggests that there is a real lack of morphological synapomorphy/autapomorphy within the continental genera because many species groups and species are likewise defined only by unique combinations of homoplastic characters states, not unique states.

Distribution in relation to phylogenetic results and homoplasy.—Because the oldest islands in the archipelago are in the southeast and the youngest in the west and northwest, correlation of geology with the cla-

dograms is not straightforward. If the species diverged from east to west, the basal split should produce a group of eastern species with the western species the most derived. However, the main split is between lowland and upland species. This may suggest that the lowland species diverged after the older islands from San Cristóbal west to Santiago were already in place and the lineage ancestors were able to disperse among islands easily. Among the upland species, *Scalesia microcephala* and *S. cordata* (basal in some results) occur on the youngest islands. Presumeably, *Scalesia pedunculata* was already distinct and dispersed on the older islands and founded populations on the new volcanoes that later formed Isabela to originate the two other arboreous species.

Species of *Scalesia* are characterized by nearly allopatric distributions in similar habitats (12 spp. in arid communities, 3 spp. in upland moist communities) within the archipelago. The only synapomorphy correlated with the origin of the upland-habitat lineage is the tree growth habit, though four homoplastic characters also accompany the habitat (loss of leaf adaxial strigosity, moderately sized capitula, glabrous paleae, and corolla tube glabrous). The development of arborescence in a moist habitat under reduced competition is easy to understand (see Itow 1995; Hamann 2001), but further study is needed to determine if the other apomorphies are correlated with reproductive ecology. Eight homoplastic apomorphies but no synapomorphies are correlated with origin of the lineage in the lowland habitat (pubescence strongly strigose, elliptic leaves with entire margins, solitary capitula, blunt phyllaries, paleae deeply divided into elliptic lobes, achenes lacking awns). Unless additional environmental factors, such as humidity, ion content, pollinators, or dispersers, etc. significantly differentiate among both lowland and upland habitats, the species within these two elevational zones appear to occupy nearly the same range of habitats. For example, *Scalesia villosa* is the only *Scalesia* species having a dense covering of villous hairs, which presumably functions as a protection from high solar radiation. But several species occupying such habitats are not villous even though villous hairs occur in the related genera. Although *S. helleri* bears pinnatifid leaves as an autapomorphy, the nearly parapatric and perhaps sister species is distinguished only by two homoplastic apomorphies. Only a single autapomorphy (fully winged petioles) and three homoplastic traits distinguish *S. crockeri*; nearly parapatric with it is *S. aspera*, which is differentiated by only four homoplastic traits. Furthermore, diversification among the lowland species has resulted in some sharing apomorphies with some or all of the upland species and vice versa. *Scalesia microcephala* of mesic forests shares two palea character states (see above) with *S. villosa* but not with its close congeners in the mesic zone. Thus, demonstrating adaptation of distinguishing features of these species may prove to be challenging.

Speciation Patterns.—Because the sister-group to *Scalesia* remains obscure, comparison of speciation amounts among clades is not possible. It is apparent that this situation will not change until multiple congruent lines of molecular evidence resolve the relationships of the infrageneric groups of *Viguiera* and other genera in the derived Helianthinae. However, if a DNA sequence in which there is variation among species of *Scalesia* can be found and analyzed, then, at least speciation rates within *Scalesia* should be forthcoming.

Sampling recommendations.—Given the above situation, it is clear that sampling for future phylogenetic analyses should include, in addition to the present taxa, at least species of *Tithonia*; *Viguiera* subg. *Amphilepis*, sect. *Maculatae*, and sect. *Paradosa;* and other segregate genera of the derived Helianthinae. When congruent lines of molecular evidence point to one of these lineages as sister to *Scalesia*, a complete sampling of species should be attempted to determine whether the whole lineage or a subset of species is the actual sister to *Scalesia*.

CONCLUSION

The present study provides a large morphological data set for comparison with molecular phylogenies of *Scalesia* and close relatives when the molecular data become available. The results confirm that additional taxa and DNA sequences must be sampled to resolve the intergeneric and internal relationships of *Scalesia*. Furthermore, divergence of *Scalesia* from its origin to terminal speciations is characterized by combinations of homoplastic apomorphies. Likewise divergence and inter-island geography appear to be poorly correlated. The seeming uniformity within habitat zones, though, appears to be correlated with the homoplasy associated with divergence in *Scalesia*. Determining the degree to which these homoplastic morphological apomorphies are adaptive should clarify the process of speciation in this and other island endemics.

APPENDIX

Data matrix. Missing, unknown, or inapplicable=? polymorphic characters indicated by symbols as follows: A={01} B={02} C={03} D={04} E={05} F={12} G={13} H={14} I={15} J={23} K={24} M={35} N={012} P={013} Q={015} R={023} S={024} T={124} U={234} V={0123} X={2345} Y={01234}.

										1										2										3										4										5										6			
Taxa	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3
Sc_helleri	0	0	1	0	0	1	0	4	0	0	1	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	2	1	1	A	2	4	N	0	3	0	1	1	0	1	2	0	0	1	1	0	0	0	0	0	?
Sc_baurii	0	0	1	0	0	1	0	2	0	0	0	0	0	0	0	1	0	0	1	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	2	1	1	0	2	4	N	0	3	2	1	0	0	1	2	0	0	1	1	0	0	0	0	0	?
Sc_retroflexa	0	0	1	0	0	1	0	A	2	0	1	1	1	0	0	1	0	0	1	0	0	1	1	0	0	0	0	A	0	0	0	0	0	0	1	2	1	0	2	1	A	1	2	4	1	0	3	0	1	1	0	1	2	0	0	1	1	0	0	0	0	0	?
Sc_incisa	0	0	1	0	0	1	0	J	0	0	0	0	0	0	0	1	0	0	1	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	1	2	1	0	0	1	1	0	2	4	F	0	3	0	1	1	0	1	2	0	0	1	1	0	0	0	0	0	?
Sc_affinis	0	0	1	0	0	1	4	0	F	0	0	0	0	0	0	0	0	2	1	0	0	1	1	0	0	0	0	A	0	0	0	A	0	0	1	1	A	0	N	1	A	1	2	C	N	1	3	0	A	0	0	1	2	0	0	1	1	0	0	F	A	0	0
Sc_crockeri	0	2	1	0	0	1	4	0	N	0	1	1	0	0	0	0	0	3	1	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	?	?	?	?	1	1	2	0	0	1	3	2	1	1	0	1	2	0	0	1	1	0	0	F	A	0	0
Sc_aspera	0	2	1	0	0	1	4	0	N	0	F	F	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	?	?	?	?	1	0	2	0	0	0	3	0	1	1	0	1	2	0	0	1	1	0	0	F	A	0	0
Sc_divisa	0	2	0	0	0	1	3	A	2	0	1	1	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	?	?	?	?	1	1	2	0	0	0	3	2	1	1	0	1	2	0	0	1	1	0	0	F	A	0	0
Sc_gordilloi	0	2	1	0	0	1	3	0	A	0	1	1	0	0	0	1	0	0	1	0	0	2	1	1	0	0	0	0	0	0	0	0	0	0	1	0	?	?	?	?	1	1	2	0	0	0	3	2	1	1	0	1	2	0	0	1	1	0	0	F	A	0	0
Sc_atractyloides	0	0	1	0	0	1	5	0	0	0	0	0	0	0	0	0	0	1	A	0	0	1	1	0	3	0	1	0	0	A	0	0	1	A	2	0	?	?	?	?	0	1	2	0	0	0	3	2	1	1	0	1	2	0	0	1	1	0	0	0	0	0	?
Sc_stewartii	0	0	1	0	0	1	5	0	0	0	1	0	1	0	0	0	0	1	0	0	B	1	1	0	3	0	1	0	0	A	0	0	1	0	1	0	?	?	?	?	0	1	2	0	0	0	3	2	1	0	0	1	2	0	0	1	1	0	0	0	0	0	?
Sc_villosa	0	1	1	0	0	1	5	0	0	0	0	0	2	0	0	0	0	2	0	0	0	1	1	0	2	0	0	0	0	0	1	0	1	0	1	0	?	?	?	?	0	1	1	1	0	1	3	0	1	1	0	1	2	0	0	1	1	0	0	0	0	0	?
Sc_cordata	1	0	0	0	0	1	2	0	1	0	0	F	B	0	0	0	0	0	1	0	1	3	1	0	A	0	0	0	0	0	0	0	1	0	1	0	?	?	?	?	1	0	1	1	0	0	3	2	1	0	0	1	2	0	0	1	1	0	0	2	2	A	0
Sc_microcephala	1	0	A	0	0	1	F	0	1	0	0	F	A	0	0	0	0	0	1	0	1	3	1	0	A	0	0	0	0	0	0	0	1	0	1	0	?	?	?	?	0	1	1	1	0	1	3	2	1	0	0	1	2	0	0	1	1	0	0	2	2	0	0
Sc_pedunculata	1	0	1	0	0	1	1	0	A	0	A	A	0	0	0	0	0	0	1	0	0	1	1	0	A	0	0	A	0	0	0	0	1	0	1	0	?	?	?	?	1	0	2	2	N	0	3	2	1	0	0	1	2	0	0	1	F	0	0	2	1	0	0
B_deltoidea	A	B	1	0	0	1	R	0	2	0	1	0	0	0	0	0	0	0	A	0	1	2	0	1	2	0	0	1	0	0	0	0	1	1	2	1	0	1	0	0	1	1	0	1	0	1	0	1	0	1	0	3	0	0	0	0	F	1	0	2	2	1	0
B_parishii	0	B	1	0	0	1	R	0	2	0	1	1	0	0	0	0	0	0	0	0	0	2	0	1	2	0	0	1	0	0	0	0	1	1	2	1	0	1	0	0	0	0	0	1	0	1	0	1	0	1	0	3	0	0	0	0	1	1	0	2	2	0	0
V_adenophylla	0	B	0	0	0	1	J	0	2	0	1	1	0	0	0	0	0	0	1	0	1	2	0	1	2	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	G	0	0	2	0	A	1	0	1	0	0	0	1	1	1	0	B	C	0	1
V_cordifolia	J	2	0	0	1	1	B	0	1	0	1	1	0	0	0	0	0	A	0	0	F	2	0	0	K	0	0	0	1	0	0	1	1	1	1	1	0	0	0	1	1	1	A	1	3	1	0	1	1	1	2	0	0	0	1	1	F	1	0	2	2	1	0
V_grammatogl.	0	1	1	0	1	2	2	0	1	0	0	0	1	0	0	0	0	0	1	1	2	2	1	1	0	0	0	0	F	0	0	1	A	A	1	1	0	0	0	1	1	1	A	1	C	1	0	0	1	1	0	0	0	0	1	1	1	1	1	2	2	1	1
V_stenoloba	0	A	1	0	A	1	M	D	0	1	0	0	1	0	0	A	0	3	1	0	0	2	0	0	3	0	1	0	1	1	0	0	1	1	F	1	0	0	A	1	2	1	A	F	C	1	0	2	1	1	2	0	0	0	1	1	0	0	1	0	0	0	?
Si_ghiesbre.	2	A	0	0	1	1	C	0	F	0	0	1	0	0	0	0	0	4	1	1	1	2	0	A	2	0	0	A	2	0	0	1	1	A	0	1	0	0	A	1	0	1	A	G	0	1	0	1	1	0	2	1	0	0	1	1	A	A	F	B	B	A	0
Si_santoros.	2	0	0	0	1	1	0	0	F	0	1	1	0	0	1	0	0	0	0	1	F	2	0	0	2	0	0	1	B	0	0	1	1	0	0	1	0	0	A	1	0	1	A	1	0	1	0	1	1	0	2	A	0	0	1	1	F	A	2	2	2	0	0
Si_fruticulosa	B	A	1	0	1	1	C	Y	F	0	1	2	0	0	0	0	0	4	A	1	F	2	0	0	2	0	0	1	B	0	0	1	1	0	0	1	0	0	A	1	0	1	A	1	0	1	0	A	1	0	2	A	0	0	1	1	F	A	2	B	B	0	0
Si_mollinae	B	0	1	0	1	1	C	Y	F	0	0	0	0	0	0	0	0	4	1	1	F	2	0	0	2	0	0	1	0	0	0	1	1	0	0	1	0	A	A	1	0	1	A	1	0	1	0	0	1	0	2	A	0	0	1	1	F	A	2	2	2	0	0
Si_holwayi	B	0	1	0	1	1	C	N	F	0	0	0	0	0	0	0	0	4	1	1	F	2	0	0	2	0	0	1	G	0	0	1	1	0	0	1	0	0	A	1	0	1	A	1	0	1	0	0	1	0	2	0	0	0	1	1	F	A	2	2	2	0	0
Si_steyerm.	B	B	1	0	1	1	C	0	1	0	0	0	0	0	0	0	0	4	1	1	2	2	0	0	2	0	0	1	B	0	0	1	1	0	0	1	0	0	A	1	0	1	A	1	0	1	2	1	1	0	2	A	0	0	1	1	1	A	2	B	B	0	0
Si_annectens	B	2	1	0	1	1	C	Y	F	0	1	1	0	0	0	0	0	Y	1	1	F	2	0	0	2	0	0	A	R	0	0	1	1	A	0	1	0	0	A	1	0	1	A	1	0	1	2	1	1	0	2	A	0	0	1	1	F	A	2	B	B	0	0
Si_tenuis	U	0	1	0	1	1	C	A	1	0	0	0	0	0	0	0	0	4	A	1	F	2	0	0	2	0	0	1	C	0	0	1	1	0	0	1	0	0	A	1	0	1	A	1	0	1	0	A	1	0	2	A	0	0	1	1	F	A	2	0	0	0	?
Si_villasenorii	B	2	1	0	1	1	C	0	F	0	1	1	0	0	1	0	0	4	A	1	F	2	0	0	2	0	0	1	C	0	0	1	1	0	0	1	0	0	A	1	0	1	A	1	0	1	2	A	1	0	2	A	0	0	1	1	2	A	2	2	2	A	0
Si_setosa	J	0	1	0	1	1	C	Y	F	0	0	0	0	0	0	0	0	4	1	1	F	2	0	0	2	0	0	1	C	0	0	1	1	0	0	1	0	0	A	1	0	1	A	1	0	1	2	1	1	0	2	A	0	0	1	1	2	A	2	B	B	0	0
Si_sanguinea	J	2	1	0	1	1	Q	Y	F	0	1	A	0	0	0	0	0	V	A	1	F	2	0	A	2	0	0	A	R	0	0	1	1	A	0	1	0	0	A	1	0	1	A	1	0	1	X	A	1	0	2	B	1	0	1	1	F	A	2	B	B	A	0
Si_calva	J	2	1	0	1	1	0	Y	F	0	1	1	0	0	0	0	0	4	A	1	0	F	0	0	2	0	0	A	B	0	0	1	1	A	0	1	0	0	A	1	0	1	A	1	0	1	E	A	1	0	2	A	0	0	1	1	F	A	2	N	B	0	0
Si_lagasciformis	4	B	1	0	1	1	C	Y	F	0	A	A	0	0	0	0	0	4	1	1	F	K	0	A	2	0	0	1	C	0	0	1	1	0	0	1	0	0	A	1	0	1	A	G	0	1	0	A	1	0	2	2	0	0	1	1	F	A	2	B	B	0	0
Si_eurylelpis	4	0	0	0	1	1	0	Y	F	0	0	0	0	0	0	0	0	4	1	1	F	2	1	0	2	0	0	1	C	0	0	1	1	0	0	0	?	?	?	?	0	1	A	1	0	1	0	0	1	0	2	0	0	0	1	1	F	A	2	B	B	0	0
Si_chaseae	4	0	1	0	1	1	C	N	F	0	0	0	0	0	0	0	0	4	1	1	F	2	1	0	2	0	0	1	0	0	0	1	1	0	0	1	0	0	A	1	0	1	A	1	0	1	2	A	1	0	2	0	0	0	1	1	F	A	2	B	B	0	0

Si_dombeyana	4 B 1 0 1 1 C N F 0 1 1 0 0 0 0 0 4 1 1 1 2 1 0 2 0 0 0 0 0 0 1 1 0 0 1 0 0 A 1 0 1 A 1 0 1 2 0 1 0 2 A 0 0 1 1 2 A 2 2 2 A 0
Si_amplexic.	4 2 1 0 1 1 C Y F 0 1 1 0 0 0 0 0 V 1 1 F 2 0 A 2 0 0 0 2 0 0 1 1 1 0 1 0 0 A 1 0 1 A 1 0 1 0 0 1 0 2 2 0 0 1 1 F A 2 B B 0 0
Si_foetida	4 A 1 0 1 1 C Y F 0 A A 0 0 0 0 0 Y 1 1 0 F 0 A 3 0 0 0 0 1 0 1 1 A 0 1 0 0 A 1 0 1 A 1 0 1 B A 1 0 2 A 0 0 1 1 F A 2 2 2 A 0
P_matthewsii	0 1 1 0 0 1 A 0 A 0 F 0 1 0 0 0 0 1 1 0 1 2 A 0 B 0 A A 1 0 A 0 A A 2 1 0 0 A 1 A 0 A 1 A 1 0 0 1 1 0 0 0 0 0 0 A 1 0 2 2 A 1
P_sagasteguii	0 1 1 0 0 1 C 0 2 0 F 0 2 0 0 0 0 0 1 0 1 2 1 0 2 0 0 0 1 0 0 0 1 1 2 1 0 0 0 1 A 0 1 1 1 1 0 0 0 1 0 0 0 0 0 0 A A 0 2 2 A 1
P_ecuadoriensis	0 F 1 0 0 1 P 0 F 0 1 1 1 0 0 0 0 0 1 0 1 2 0 0 2 0 0 0 1 0 0 0 A 0 2 1 0 0 0 1 0 1 A 1 0 1 0 0 0 1 0 0 C 0 0 0 A A 0 2 2 A 1
P_hutchisonii	0 A 1 0 0 2 0 0 A 0 0 0 1 0 0 0 0 1 1 0 1 2 0 0 4 0 0 1 1 0 0 0 0 1 2 1 1 1 0 1 1 1 1 3 A 1 0 1 A 1 0 0 0 0 0 0 1 1 0 2 2 1 1
P_acutifolius	0 N 1 0 0 1 I 0 A 0 1 1 0 0 0 0 0 1 A 0 1 F 1 0 2 0 1 1 1 0 0 0 1 1 2 1 0 0 0 1 A 0 0 1 1 1 0 0 1 1 0 0 0 0 0 0 1 1 0 2 2 1 1
P_verbesinoides	0 F 1 0 0 2 1 0 0 0 F 0 2 0 0 0 0 1 0 0 1 2 0 0 B 0 0 0 1 0 0 0 0 0 2 1 0 0 0 1 0 0 0 1 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 2 2 0 1
P_hypargyreus	0 N 1 A 0 1 R 0 F 0 1 1 0 0 0 0 0 1 1 0 1 1 1 0 1 0 1 1 1 1 1 0 1 1 2 1 0 0 0 1 0 1 0 1 0 1 0 0 0 1 0 A C 0 0 0 1 A 0 2 2 1 1
P_imbaburensis	0 B 1 A 0 1 A 0 N 0 1 1 1 0 0 0 0 1 1 0 1 2 0 0 B 0 0 1 2 0 0 0 0 A 2 1 0 0 0 1 0 0 0 1 0 1 0 0 0 1 0 0 C 0 0 0 A 0 0 2 2 1 1
P_juncosae	0 F 1 0 0 1 0 0 1 0 1 1 1 0 0 0 0 1 A 0 1 1 0 0 0 0 1 1 1 0 1 0 0 A 2 1 0 0 0 1 0 0 0 1 A A 0 0 0 1 0 0 C 0 0 0 2 0 0 2 2 0 1
P_lehmannii	0 1 1 0 0 0 R 0 F 0 1 F 0 0 0 0 0 1 A 0 1 1 1 0 S 0 1 1 F 1 1 0 A A 2 1 0 1 0 0 0 0 0 1 C 1 0 0 0 A 1 1 0 1 0 0 2 0 0 2 2 A 1
P_nigrescens	0 F 1 1 0 1 C 0 F 0 1 F A 0 0 0 0 0 1 0 1 1 1 2 S 0 0 1 2 0 0 0 0 A 2 1 0 F 0 0 0 0 0 1 C 1 0 0 1 1 1 1 0 1 0 0 1 0 0 2 2 1 1
P_andinus	0 A 1 0 0 2 0 0 1 0 0 0 2 0 0 0 0 0 0 0 B 1 1 0 S 0 1 1 2 0 0 0 0 A 2 1 0 1 0 0 A 0 0 1 0 1 0 0 0 1 1 1 0 0 0 0 1 0 0 2 2 0 1
P_storkhorton.	0 F 1 1 0 1 0 0 1 0 1 F 0 0 0 0 0 0 1 0 1 1 1 0 S 0 1 1 2 0 0 0 1 1 2 1 ? 1 0 0 0 A 0 1 C 1 0 0 0 1 1 1 0 0 0 0 1 0 0 2 2 0 1
P_acuminatus	0 F 1 0 1 1 C 0 0 0 F 0 F 0 0 0 0 0 1 1 1 1 1 0 E 0 0 1 2 0 0 0 0 0 2 1 0 1 0 0 A 0 0 1 0 1 0 0 1 1 1 1 1 0 0 0 1 0 0 2 2 0 1
P_cinerascens	0 F 1 0 1 1 A 0 1 0 1 1 1 0 0 0 0 0 1 A 1 1 1 0 B 0 0 1 2 A 0 0 1 1 2 1 1 F 0 0 0 0 0 1 C 1 0 A A 1 1 1 1 0 0 0 1 0 0 2 J 0 1
P_mollicomus	0 F 1 0 A 1 H 0 1 0 1 0 F 0 0 0 0 1 1 1 A 1 1 0 S 0 0 1 2 0 1 0 0 A 2 1 1 1 0 0 0 0 0 1 C 1 0 0 0 1 1 1 0 0 0 0 1 0 0 2 3 0 1
P_macranthus	0 F 1 0 A 1 A 0 2 0 1 A 0 0 0 0 0 0 0 1 1 1 1 1 2 2 0 1 0 2 1 0 0 1 1 2 1 0 F 0 1 A 0 0 F C A 0 0 0 1 1 1 0 0 0 0 1 0 0 2 3 0 1
P_sanchezii	1 F 1 0 1 0 0 0 1 0 1 0 1 0 0 0 0 0 1 A A 0 1 0 2 0 1 0 1 1 0 0 1 1 2 1 0 1 0 0 2 0 0 2 C A 0 0 1 0 1 1 0 0 0 0 1 0 0 2 2 0 1
P_youngiorum	0 N 1 0 1 1 0 0 A 0 1 1 0 0 0 0 0 0 A A 1 0 1 0 2 0 1 1 1 1 0 0 1 1 2 1 0 F 0 0 1 1 0 F 0 A 0 0 0 1 1 1 1 0 0 0 1 0 0 2 2 0 1
P_schillingii	0 N 1 0 1 0 C 0 F 0 1 0 2 0 0 0 0 0 A 0 1 1 1 0 2 A 1 1 1 1 0 0 1 1 2 1 0 A 0 0 A 0 0 F C A 0 0 0 1 1 1 C 0 0 0 1 0 0 2 2 0 1
P_amoenus	0 A 1 0 1 1 P 0 N 0 0 0 F 0 0 0 0 A A 1 A 0 1 0 0 A 0 1 1 0 0 0 0 1 2 1 1 0 0 0 1 A 0 F C A 0 0 1 1 1 1 1 0 0 0 0 A 1 0 2 2 A 1
P_robinsonii	0 1 1 A A 1 A 0 1 0 1 0 2 0 0 0 0 1 1 1 1 0 1 2 0 1 1 1 1 A A 0 0 A 2 1 1 1 0 0 1 0 0 1 0 1 0 1 1 1 1 1 1 0 0 0 1 A 0 2 2 A 1
P_steubelii	1 F 1 A 0 0 A 0 A 1 1 0 2 0 1 0 0 0 1 0 0 0 1 2 2 0 1 0 ? 0 1 0 1 0 2 1 0 F 0 0 0 0 0 1 0 1 0 0 0 1 1 1 1 0 0 0 1 0 0 2 2 0 1
P_smithii	0 1 1 0 0 0 A 0 0 1 1 0 2 0 1 0 0 0 A 0 B 1 1 2 2 0 1 1 2 1 1 0 1 1 2 1 0 1 0 0 0 0 0 F C A 0 0 A 1 1 1 1 0 0 0 1 0 0 2 2 0 1
P_jelskii	0 N 1 A 1 0 A 0 0 1 A A 2 0 1 0 0 0 A 1 F 0 1 2 2 0 1 1 2 1 A 0 1 1 2 1 0 0 0 0 0 0 0 F C A 0 0 A 1 1 1 C 0 0 0 1 0 0 2 2 0 1
P_lodicatus	0 F 1 1 0 0 0 0 0 1 1 0 2 0 1 0 0 1 1 0 A 1 1 0 B 0 0 1 2 0 0 0 0 0 2 1 0 1 0 0 A 0 0 1 0 1 0 0 0 1 1 1 C 0 0 0 1 0 0 2 2 0 1
P_microphyllus	0 F 1 0 0 0 Q 0 0 1 1 0 2 0 1 A 0 1 0 0 0 2 0 0 R 0 0 A 1 0 0 0 0 0 2 1 0 0 0 0 A 0 0 1 0 1 0 0 0 1 1 1 C 0 0 0 A 0 0 2 2 0 1
P_subniveus	0 F 1 0 A 0 I 0 0 1 F 0 2 0 1 0 0 0 0 0 0 0 1 0 0 R 0 1 1 ? 0 1 0 1 A 2 1 0 A 0 0 0 0 0 1 C 1 0 1 0 1 1 1 A 0 0 0 1 A 0 2 2 A 1
P_cajamarcensis	0 1 1 0 0 0 1 0 0 1 0 0 2 1 1 0 0 0 0 0 A 1 A 0 B 0 1 1 ? 0 1 0 1 A 2 1 0 1 0 0 0 0 0 1 C 1 0 1 0 1 1 1 0 0 0 0 1 0 0 2 2 0 1
P_discolor	0 F 1 0 A 1 5 0 0 1 1 0 2 A 1 A 1 0 0 A 0 2 A 0 2 0 0 1 2 0 A 0 1 0 2 1 0 0 0 0 1 0 0 1 0 1 0 1 0 A 1 1 1 0 0 0 1 0 0 2 2 0 1
P_decumbens	0 2 1 0 0 0 5 0 0 1 1 0 2 1 1 1 0 2 0 0 0 2 A 0 2 0 0 0 2 0 0 0 1 A 2 1 0 0 0 0 1 0 0 1 C 1 0 1 0 A 1 1 0 0 0 0 1 0 0 2 3 0 1
P_woodsonianus	0 2 1 0 1 0 4 0 0 1 1 0 2 0 1 0 0 0 0 1 B 1 1 0 0 0 0 1 2 0 0 0 0 0 2 1 0 0 0 0 1 0 0 1 C 1 0 0 0 A 1 1 0 0 0 0 1 0 0 2 3 0 1
P_davidii	0 F 1 0 0 0 1 0 1 1 1 1 0 0 1 0 0 0 0 0 A 1 1 0 2 0 0 1 2 0 0 0 1 A 2 1 0 A 0 1 1 0 0 1 0 1 0 0 0 1 1 1 1 0 0 0 1 0 0 2 2 0 1
P_lanatus	0 F 1 0 1 0 A 0 0 1 1 0 2 0 1 0 0 0 0 0 1 1 A 0 T 0 0 1 2 0 0 0 0 A 2 1 0 1 0 0 A 1 0 1 0 1 0 0 0 A 1 1 1 0 0 0 1 0 0 2 2 0 1
P_argenteus	0 F 1 0 A 0 1 0 A 1 1 0 F 0 1 0 0 1 0 0 0 2 1 0 0 0 0 1 2 0 0 0 0 1 2 1 0 1 0 0 1 1 0 1 0 1 0 0 0 0 1 1 0 0 0 0 F 0 0 2 2 A 1
P_viridior	0 F 1 0 0 0 1 0 A 1 1 0 F 0 1 0 0 1 0 0 0 1 A 0 S 0 1 1 0 0 0 0 A 1 2 1 A A 0 0 0 0 0 0 1 0 1 0 1 0 0 1 1 C 0 0 0 1 0 0 2 2 0 1
P_senex	0 F 1 0 1 2 0 0 A 1 1 0 2 0 1 0 0 0 1 0 1 2 0 0 0 0 0 0 0 0 0 0 0 0 0 2 1 0 0 0 0 1 1 0 1 0 1 0 0 0 A 1 1 1 0 0 0 1 0 0 2 2 0 1
H_annuus	4 B 1 0 0 1 B 0 F 0 1 1 0 0 0 0 0 A 1 0 0 A 1 B 1 0 1 0 0 1 0 1 1 1 1 1 0 F 0 1 2 1 1 3 0 1 0 0 1 1 2 3 A 0 1 1 2 1 0 2 2 A 1
H_tuberosus	3 B 1 0 1 1 1 0 1 0 1 1 0 0 0 0 0 2 1 0 1 1 1 1 1 0 1 0 2 1 0 1 1 1 1 1 0 F 0 1 2 1 1 1 0 1 0 1 0 1 0 3 0 0 1 1 2 A 0 2 2 A 1

ACKNOWLEDGEMENTS

We thank Todd Wood for encouragement and comments and Stephanie Mace for assistance with graphics. The herbaria BRIT, SMU, and VDB are thanked for the loan and use of specimens as is Amanda Neill, Botanical Research Institute of Texas, for expediting those loans to Bryan College.

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BOOK REVIEW

Peggy Kochanoff. 2009. **You Can Be a Nature Detective.** (ISBN 978-087842556-3, pbk.). Mountain Press Publishing Company, P.O. Box 2399, Missoula, Montana 59806, U.S.A. (**Orders:** www.mountain-press.com, info@mtnpress.com, 1-800-234-5308). $14.00, 63 pp., 9" × 8 3/8".

You Can Be a Nature Detective is a great little book for parents, teachers, grandparents, and any others interested in spending time with children out of doors. It begins with an attention-grabbing opener ("Hmmm... there's spit all over the grass. Who could have done it?") and proceeds to answer or solve this and other outdoor "mysteries." Although some of these mysteries are only found in limited geographic regions (say, where an actual snowy winter occurs), all are wonderfully engaging and entertaining. Through the process of solving nature riddles (Why are the leaves changing colors? Will that creepy crawly thing turn into a butterfly or moth? What's that fuzzy stuff on the ground?) the author has highlighted 12 different visual clues that can be further investigated by a curious child. A detailed explanation accompanies each mystery and these are further enhanced with beautiful watercolor illustrations.

At the end of the book are some additional "Fun Things to Do in Nature" (each related to one of the former mysteries), such as counting different frog calls, making prints of spider webs, and dissecting owl pellets, as well as a glossary and list of suggested resources. Despite the fact that it is written at an age-appropriate level for kids to read and enjoy, I see *You Can Be a Nature Detective* more as a vehicle for an adult to spend quality time in nature with a child. It's a ready-made, go-to source for those times when the kids are saying, "I'm bored!," a source that no parent or grandparent should be without.—*Palmer Byerley, Elementary Science Teacher, Crowley, Texas, U.S.A.*

Ms. Kochanoff's book is part field guide and part nature journal. It offers good information about a variety of plants and animals with well-executed watercolor illustrations. However, contrary to the title, the reader doesn't have to be a detective at all when the answers to the questions asked are immediately given. She doesn't make it clear if the reader is participating in real hands-on outdoor investigations as a "nature detective" or just reading another informational nature field guide. A good concept but is lacking in engaging mystery.—*Pam Chamberlain, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

INTRODUCED LESSER CELANDINE (*RANUNCULUS FICARIA*, RANUNCULACEAE) AND ITS PUTATIVE SUBSPECIES IN THE UNITED STATES: A MORPHOMETRIC ANALYSIS

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ABSTRACT

Ranunculus ficaria is native to Europe, but was introduced to the United States by at least the 19th century as a garden ornamental. Following introduction, the species escaped from cultivation. Because, in contrast to European floristic treatments, previous North American floristic treatments had not emphasized subspecific recognition, our objectives for this study were to determine if and how many morphologically recognizable entities within *R. ficaria* occur in the United States, evaluate to what extent such entities correspond to the subspecific concepts followed in Europe, and analyze the distributions, habitats, and rates of spread of each entity. To meet our objectives, we conducted a morphometric analysis based on study of 319 specimens from forty-seven herbaria. The combined results indicate the presence of five entities reasonably referable to the subspecies accepted in Europe. If one accepts subspecies as incompletely diverged lineages, one would expect a limited amount of overlap of operational taxonomic units (OTUs) as seen in our Principal Coordinates Analysis and Principal Components Analysis results, as well as incompletely sorted OTUs as seen in our cluster and classification tree analyses. Based on our current understanding, all five subspecies occur in the United States. They are best adapted to moist sites, exhibit overlapping distributions, and appear to be spreading at similar rates.

RESUMEN

Ranunculus ficaria es nativa de Europa, pero fue introducida en los Estados Unidos como ornamental en el siglo XIX. Después de la introducción, la especie escapó de cultivo. Porque, en comparación con los tratamientos florísticos europeos, los norteamericanos no habían enfatizado en el reconocimiento subespecífico, nuestros objetivos en este estudio fueron determinar si existen y cuantas entidades reconocibles morfológicamente de *R. ficaria* se dan en los Estados Unidos, evaluar en que medida tales entidades corresponden al concepto de subespecie que se sigue en Europa, y analizar las distribuciones, hábitats, y tasas de expansión de cada entidad. Para lograr nuestros objetivos, realizamos un análisis morfométrico basado en el estudio de 319 especímenes de cuarenta y siete herbarios. Los resultados combinados indican la presencia de cinco entidades razonablemente referibles a las subespecies aceptadas en Europa. Si se aceptan subespecies como líneas divergentes incompletas, se podría esperar una cantidad limitada de solapamiento en las unidades taxonómicas operativas (OTUs) como aparecen en nuestro Análisis de Coordenadas Principales y Análisis de Componentes Principales, así como OTUs incompletamente ordenados como se ven en nuestros análisis de clusters y árboles de clasificación. Basados en nuestro conocimiento presente, las cinco subespecies están en los Estados Unidos. Están mejor adaptadas a lugares húmedos, muestran distribuciones que se solapan, y parece que se extienden a velocidades semejantes.

INTRODUCTION

Ranunculus ficaria L. (Ranunculaceae) is native to Europe (Tutin 1964; Taylor & Markham 1978; Sell 1994; Whittemore 1997), but was introduced to the United States (U.S.) through the garden ornamental trade for its showy flowers (Bailey 1935). It was collected with certainty in the U.S. in 1867 (Philadelphia County, Pennsylvania, *Burke s.n.*, PH) and required 141 years to "spread" from Philadelphia, Pennsylvania to Fort Worth, Texas (*Nesom FW08-1*, BRIT, MO, NCSC, NCU, TEX)—the southernmost extent of the current known distribution (Nesom 2008).

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J. Bot. Res. Inst. Texas 3(1): 193 – 209. 2009

In Europe, five subspecies of *Ranunculus ficaria* are recognized (Tutin 1964; Sell 1994), whose "ecology and [. . .] distribution appear to overlap, but tend to be different" (Sell 1994). *Flora Europaea* currently recognizes: (1) *Ranunculus ficaria* subsp. *ficaria* from western Europe, eastward to southern Italy, (2) subsp. *bulbilifer* Lambinon from northern and central Europe, extending to Spain, Albania and east-central Russia, (3) subsp. *calthifolius* (Reichenb.) Arcangeli from south-central and eastern Europe, (4) subsp. *chrysocephalus* P.D. Sell from Greece and Crete, and (5) subsp. *ficariiformis* (F.W. Schwartz) Rouy & Fouc from southern Europe. Plants are known to be diploid (2n=16), triploid (2n=24), or tetraploid (2n=32). Diploids have been referred to subspecies *calthifolius* and *ficaria*, and tetraploids to *bulbilifer*, *chrysocephalus*, and *ficariiformis* (Greilhuber 1974; Sell 1994). Triploids may represent putative hybrids and have apparently been collected from widely separated localities in Europe (Marchant & Brighton 1974; Sell 1994). Sell (1994) suggested that a large proportion of the pollen of triploids, as well as the tetraploid subsp. *bulbilifer*, is non-viable and few seeds are set. Pollen from diploids and the large-flowered tetraploids (i.e., *chrysocephalus* and *ficariiformis*) is apparently viable and many achenes are produced (Sell 1994). Two subspecies are capable of producing bulbils in their leaf axils: *bulbilifer* and *ficariiformis*. Subspecies *bulbilifer* tends to exhibit globose bulbils and subsp. *ficariiformis* produces ellipsoid bulbils (Sell 1994).

In contrast to European accounts, North American floristic treatments either recognized no subspecific taxa in *R. ficaria* (Fernald 1950; Gleason 1952; Gleason & Cronquist 1963; Whittemore 1997) or only variety *bulbifera* Marsden-Jones (=subsp. *bulbilifer* Lambinon; Magee & Ahles 1999). However, the recent discoveries of entities putatively referable to subsp. *ficariiformis* in North Carolina (Krings et al. 2005) and Texas (Nesom 2008; reported as subsp. *bulbilifer*, but with ellipsoid bulbils and flower dimensions within the range of *ficariiformis*) caused us to question whether additional subspecies may be present in North America that have not been previously recorded and if so, whether these differed in their distributions, habitats, and rates of spread. Because prior North American treatments did not emphasize subspecific recognition and as subspecies are not uniformly accepted, our objectives were to: (1) determine if and how many morphologically recognizable entities within *R. ficaria* occur in the United States, (2) evaluate to what extent such entities correspond to the subspecific concepts followed in Europe (based on the work of Sell 1994), and (3) analyze the distributions, habitats, and rates of spread of each entity.

METHODS

Distribution and habitat information were recorded from 319 herbarium specimens, requested from the following forty-seven herbaria based on previous literature reports (Benson 1942; Bell 1945; Gleason & Cronquist 1991; Whittemore 1997): A, AUA, BALT, BH, BKL, BRIT, CONN, CU, DOV, F, FLAS, GA, GH, HNH, ILLS, KE, LGO, LSU, MARY, MASS, MICH, MISS, MO, MOR, MSC, MT, MU, NA, NCSC, NCU, NHA, NY, OS, OSC, PH, POM, TENN, TEX, UNA, US, USF, USCH, VDB, VPI, WTU, WVA, Y (Appendix A). Herbarium label data recorded for each specimen included collector name, collector number, date, habitat, and county and state of collection. Specimens lacking information were excluded from the study.

Collection localities were classified into the following nine habitat classes: (1) adjacent to a water source, (2) disturbed areas, (3) dry woods, (4) fields, (5) horticultural, (6) lawns, (7) lowlands, (8) moist areas, and (9) roadsides. A specimen was classified as adjacent to a water source if it was collected along the banks of a river, stream, or pond. Moist areas were defined as moist or alluvial woods, swamp or bog areas, and other moist shade. The horticultural class was defined as being collected in a nursery or garden under cultivation. Lowlands were defined as low or depressed areas where moisture level was not mentioned on the label. Fields were defined as any open grassy area not maintained as a lawn and in full sun such as pastures and meadows.

To determine if and how many morphologically recognizable entities within *R. ficaria* occur in the United States, each herbarium sheet was treated as an operational taxonomic unit (OTU) for data capture and pertinent subsequent analyses. To evaluate to what extent such entities correspond to the subspecific concepts followed in Europe, each specimen was determined to subspecies following the key constructed by Sell (1994):

1. Leaf blades to 8 × 9 cm; petioles to 28 cm; flowers to 60 mm diam; achenes 5.0 × 3.5 mm.
   2. Stems rather robust, but straggling; bulbils present in leaf axils after flowering ______ subsp. **ficariiformis**
   2. Stems robust and erect; without bulbils in leaf axils after flowering ______ subsp. **chrysocephalus**
1. Leaf blades to 4 × 4 cm; petioles to 15 cm; flowers to 40 mm diam; achenes to 3.5 × 2.2 mm.
   3. Leaves crowded at the base with few on short stems ______ subsp. **calthifolius**
   3. Leaves less crowded at base and more numerous on the elongate stems.
      4. Bulbils not present in leaf axils after flowering; achenes well developed ______ subsp. **ficaria**
      4. Bulbils present in leaf axils after flowering; achenes poorly developed ______ subsp. **bulbilifer**

Sell (1994) recognized the difficulty in identifying *Ranunculus ficaria* to the subspecific level, noting that specimens should be examined throughout the growing season for positive identifications. We agree with him and others (Whittemore 1997; Nesom 2008) that identification can be challenging and recognize the impact identifications have on analysis results. However, we feel reasonably confident in our subspecies assignments due in part to the quality of specimens, which facilitated taxon assignment, as well as our own field observations and phenological analyses. Of the 319 herbarium specimens examined 232 had at least a month and year date on the label and 90% of these were collected mid-April through June. Another 5% were collected in the last week of March and the remaining 5% were collected in January through mid-March. Based on date of collection, the majority of specimens examined in this study were collected late enough in the spring that they would exhibit bulbils if they were genetically capable of producing them.

Using a digital caliper, the following morphological measurements were taken from each OTU: (1) leaf length from up to ten leaves, (2) leaf width from up to ten leaves, (3) petiole length from up to ten leaves (using same leaves measured for length and width), (4) petal length from up to ten flowers, (5) petal width from up to ten flowers, (6) achene length of all achenes present, (7) achene width for all achenes present. The presence or absence of bulbils was also recorded.

Quantitative and qualitative data were studied jointly and separately. Statistic analyses, including ANOVAs and post-hoc tests (Tukey's HSD), were carried out in the statistics package R (Ihaka & Gentleman 1996; R Foundation for Statistical Computing 2008). Prior to multivariate analysis, we tested all quantitative univariate variables using the Shapiro-Willks normality test and subsequently $\log_{10}$ transformed them to minimize the influence of allometry on the results (Dufrêne et al. 1991; Almeida-Pinheiro de Carvalho et al. 2004; Pimentel et al. 2007). Gower's dissimilarity coefficient for mixed data was used to quantify resemblances between OTUs (Gower 1971). The relationships between OTUs were subsequently explored with both hierarchical agglomerative cluster analyses and principal coordinates analyses (PCoA) using the complete set of characters. Three different sorting algorithms were used to help distinguish between data-dependent and potential method-dependent differences in results, following Dickinson & Phipps (1985) and Pimentel et al. (2007): single linkage, complete linkage, and average linkage (UPGMA; Sneath & Sokal 1973).

Quantitative characters were also analyzed separately using Principal Components Analysis (PCA). PCA is an objective, correlation-based technique that allows the variance in quantitative characters to be considered simultaneously and the subsequent visualization of dispersion patterns in a number of dimensions that explain the greatest amount of variance (Sargent et al. 2004; Joly & Bruneau 2007; Pimentel et al. 2007). A Kaiser-Meyer-Olkin (KMO) test was performed prior to the PCA to assess the suitability of the data for multivariate analysis (see also Almeida-Pinheiro de Carvalho et al. 2004; Pimentel et al. 2007).

Classification trees were employed to help identify specific morphological characters that could reliably separate the OTU groups corresponding to the five putative subspecies sensu Sell (1994). Classification trees divide datasets with pre-assigned group membership into increasingly homogeneous subsets in tree-like fashion based on the included morphological traits. Recovery proceeds until the groups obtained are pure or until a dividing threshold is achieved (Joly & Bruneau 2007). For the classification tree, all morphological characters were included and quantitative data was not log transformed prior to analysis.

The distribution of *R. ficaria* was mapped based on herbarium specimens and using ArcGIS 9.2 (ESRI 2004). The rate of spread for each subspecies was determined based on the number of counties each was present in during each decade from 1860 to the present. These data were analyzed using proc mixed in SAS

9.1.3 with a critical value of 0.05 (SAS Institute 2002–2005). Note that we use "spread" in a broad sense, as we suspect that not all new county records are the result of physical movement of propagules from established parental plants, but that many may reflect novel introduction events.

RESULTS

Descriptive statistics

Table 1 provides non-transformed means and standard deviations for the seven quantitative characters measured for each group of OTUs assignable to one of five putative subspecies sensu Sell (1994) and summarizes the results of the one-way ANOVAs and subsequent post-hoc tests (Tukey's HSD) on $\log_{10}$ transformed data (see superscripts). Figure 1 exhibits box-plots showing the distribution of non-transformed quantitative measurements taken by OTU group. Significant differences in the means for each of the five groups of OTUs assigned to the subspecies sensu Sell (1994) for all seven characters were found (Table 1). Post-hoc tests (Tukey's HSD) to determine which sample means differed from which others showed that means of leaf length and petal width of the OTU group assignable to subsp. *chrysocephalus* differed significantly ($p<0.05$) from the respective means of the groups of OTUs assignable to the four other subspecies (Table 1). OTUs assignable to the diploid subsp. *calthifolius* and *ficaria* differed significantly ($p<0.05$) in mean leaf length, mean leaf width, and mean petiole length (Table 1). They did not differ significantly in mean petal length, mean petal width, mean achene length, or mean achene width. OTUs assignable to the tetraploid subsp. *bulbilifer*, *chrysocephalus*, and *ficariiformis* differed significantly ($p<0.05$) from one another in mean leaf length and mean petal width. Subspecies *bulbilifer* differed significantly ($p<0.05$) from both subsp. *chrysocephalus* and *ficariiformis* in mean leaf width, mean petiole length, and mean petal length. Subspecies *chrysocephalus* differed significantly ($p<0.05$) from subsp. *bulbilifer* in mean achene length and width, but subsp. *ficariiformis* differed neither from subsp. *chrysocephalus* nor *bulbilifer* in these characters (Table 1).

Cluster analyses

In all three cluster analyses—average, complete, and single linkage—OTUs were resolved into two large divisions, these corresponding to (1) the bulbil bearing taxa: subsp. *bulbilifer* and subsp. *ficariiformis* sensu Sell (1994) and, (2) the non-bulbil bearing taxa: subsp. *calthifolius*, subsp. *chrysocephalus*, and subsp. *ficaria* sensu Sell (1994; Fig. 2). Within these two divisions, the topologies resulting from the three different algorithms differed notably only for those resulting from single linkage. Within the *bulbilifer/ficariiformis* division, average linkage recovered a cluster predominantly composed of OTUs referable to subsp. *ficariiformis* sister to a larger cluster of OTUs predominantly referable to subsp. *bulbilifer*. Both recovered clusters contained OTUs referable to either subspecies. The complete linkage analysis recovered three clusters within the *bulbilifer/ficariiformis* division—one of OTUs predominantly referable to *ficariiformis*, nested within two composed predominantly of OTUs referable to subsp. *bulbilifer*. Single linkage similarly recovered a cluster of OTUs referable to subsp. *ficariiformis* nested within OTUs referable to subsp. *bulbilifer*. In the *calthifolius/chrysocephalus/ficaria* division, both average and complete linkage analyses recovered a cluster of OTUs predominantly referable to subsp. *ficaria* nested within clusters of OTUs predominantly referable to subsp. *calthifolius*. OTUs referable to subsp. *ficaria* did not emerge in a distinct cluster in the single linkage analysis, but rather were interspersed throughout those referable to subsp. *calthifolius*. OTUs referable to subsp. *chrysocephalus* emerged interspersed in grades of OTUs referable to subsp. *calthifolius* and subsp. *ficaria* in a sister position to the rest of the division in all three analyses.

PCoA and PCA

Consistent with cluster analysis results, two non-overlapping clusters of OTUs were recovered in the PCoA corresponding to (1) the bulbil bearing taxa: subsp. *bulbilifer* and subsp. *ficariiformis* sensu Sell (1994) and (2) the non-bulbil bearing taxa: subsp. *calthifolius*, subsp. *chrysocephalus*, and subsp. *ficaria* sensu Sell (1994; Fig. 3A). Within both of these clusters, cohesiveness was exhibited by each group of OTUs referable to one of the five subspecies sensu Sell (1994), although each group overlapped with another to some degree.

Consistent with expectations for infraspecific entities, distinct but overlapping clusters of OTUs were

Table 1. Non-transformed means and standard deviations (s.d.) of seven characters among the five putative subspecies of *Ranunculus ficaria* (format: mean (s.d.; N)). F statistic and p-values for one-way ANOVAs of $\log_{10}$ transformed data provided in ultimate two columns. Within a row, means with different superscripts differ significantly ($p<0.05$) when component values $\log_{10}$ transformed and analyzed using post-hoc tests (Tukey's HSD).

	bulbilifer	calthifolius	chrysocephalus	ficaria	ficariiformis	F	p-value
Leaf length (cm)	2.18 ^{a,d} (0.41; 82)	1.93 ^{a} (0.46; 96)	3.54 ^{b} (1.03; 6)	2.42 ^{d} (0.39; 37)	2.97 ^{c} (0.49; 12)	9.79	<0.001
Leaf width (cm)	2.83 ^{a} (0.53; 82)	2.38 ^{b} (0.54; 97)	4.33 ^{d} (1.15; 6)	2.95 ^{a,d} (0.48; 37)	3.80 ^{c,d} (0.53; 12)	10.56	<0.001
Petiole length (cm)	10.41 ^{a} (2.79; 82)	6.55 ^{b} (1.62; 97)	16.21 ^{c} (1.44; 6)	12.19 ^{a,c,d} (2.16; 37)	14.75 ^{c,d} (3.85; 12)	28.44	<0.001
Petal length (mm)	10.23 ^{a} (1.67; 75)	11.11 ^{a} (1.91; 97)	17.43 ^{b,d} (3.79; 6)	12.11 ^{a,c} (1.95; 37)	13.91 ^{c,d} (1.95; 11)	16.89	<0.001
Petal width (mm)	3.57 ^{a} (0.91; 75)	4.53 ^{b} (1.05; 97)	7.38 ^{c} (0.45; 6)	4.83 ^{b,d} (1.09; 37)	5.75 ^{d} (1.14; 11)	23.62	<0.001
Achene length (mm)	2.95 ^{a} (0.65; 53)	3.04 ^{a} (0.65; 28)	4.33 ^{b,c} (0.69; 5)	3.27 ^{a,c} (0.41; 6)	3.50 ^{a,c} (0.90; 7)	5.30	<0.001
Achene width (mm)	4.35 ^{a} (0.90; 53)	4.26 ^{a} (1.00; 28)	6.22 ^{b,c} (0.77; 5)	4.58 ^{a,c} (1.12; 6)	4.70 ^{a,c} (1.31; 7)	3.83	<0.01

exhibited in the PCA comprising all OTUs when symbol coded for a priori subspecies assignments following the infraspecific concepts of Sell (1994) (Fig. 3B). Among these, OTUs referable to subsp. *bulbilifer* exhibited the most cohesive and least diffuse cluster. In this analysis, 81% of the variation is explained by the first two axes. PC1 is positively correlated most strongly with petiole length, leaf width, and leaf length, whereas PC2 is positively correlated most strongly with petal width and petal length (Table 2).

A separate analysis of only OTUs referred to the two diploid taxa subsp. *calthifolius* and *ficaria*, resulted in two very well-defined clusters with minor overlap (Fig. 3C; Table 3). In this analysis, 73 % of variation is explained by the first two axes. PC1 is positively correlated most strongly with petiole length, leaf length, and leaf width, whereas PC2 is positively correlated most strongly with petal width and petal length (Table 3). An analysis of only OTUs referred to the tetraploid taxa—subsp. *bulbilifer*, *chrysocephalus*, and *ficariiformis*—showed evident clustering, but with greater overlap among the three a priori defined subspecies (Fig. 3D; Table 4). In this analysis, 76% of the variation is explained by the first two axes. OTUs defined a priori as subsp. *ficariiformis* occupied a central coordinate space in the tetraploid analysis, flanked along the primary axis by subsp. *chrysocephalus* to the left and *bulbilifer* to the right. PC1 is negatively correlated most strongly with petal width, leaf length, and leaf width, whereas PC2 is positively correlated most strongly with petiole length (Table 4).

Among the five subspecies of *R. ficaria* recognized by Sell (1994), only the tetraploid subsp. *bulbilifer* and *ficariiformis* are known to produce bulbils. A separate analyses of only OTUs with bulbils, showed two rather cohesive clusters with limited overlap corresponding to a priori assignment to these two subspecies sensu Sell (1994; Fig. 3E; Table 5). In this analysis, 69% of the variation is explained by the first two axes. PC1 is negatively correlated most strongly with petal width, whereas PC2 is positively correlated most strongly with petal width and petal length (Table 5). A separate analysis of OTUs without bulbils (Fig. 3f; Table 6), showed three rather cohesive clusters with limited overlap, corresponding to a priori assigned subspecies. In this analysis, 79% of the variation is explained by the first two axes. PC1 is positively correlated most strongly with petiole length, leaf width, and leaf length, whereas PC2 is positively correlated most strongly with petal width and petal length (Table 6).

Classification tree

Classification tree analysis showed that 95% or greater of the OTUs we referred to subsp. *calthifolius*, subsp. *ficaria*, and subsp. *bulbilifer* using Sell (1994) could be placed into corresponding homogeneous groups (Fig. 4).

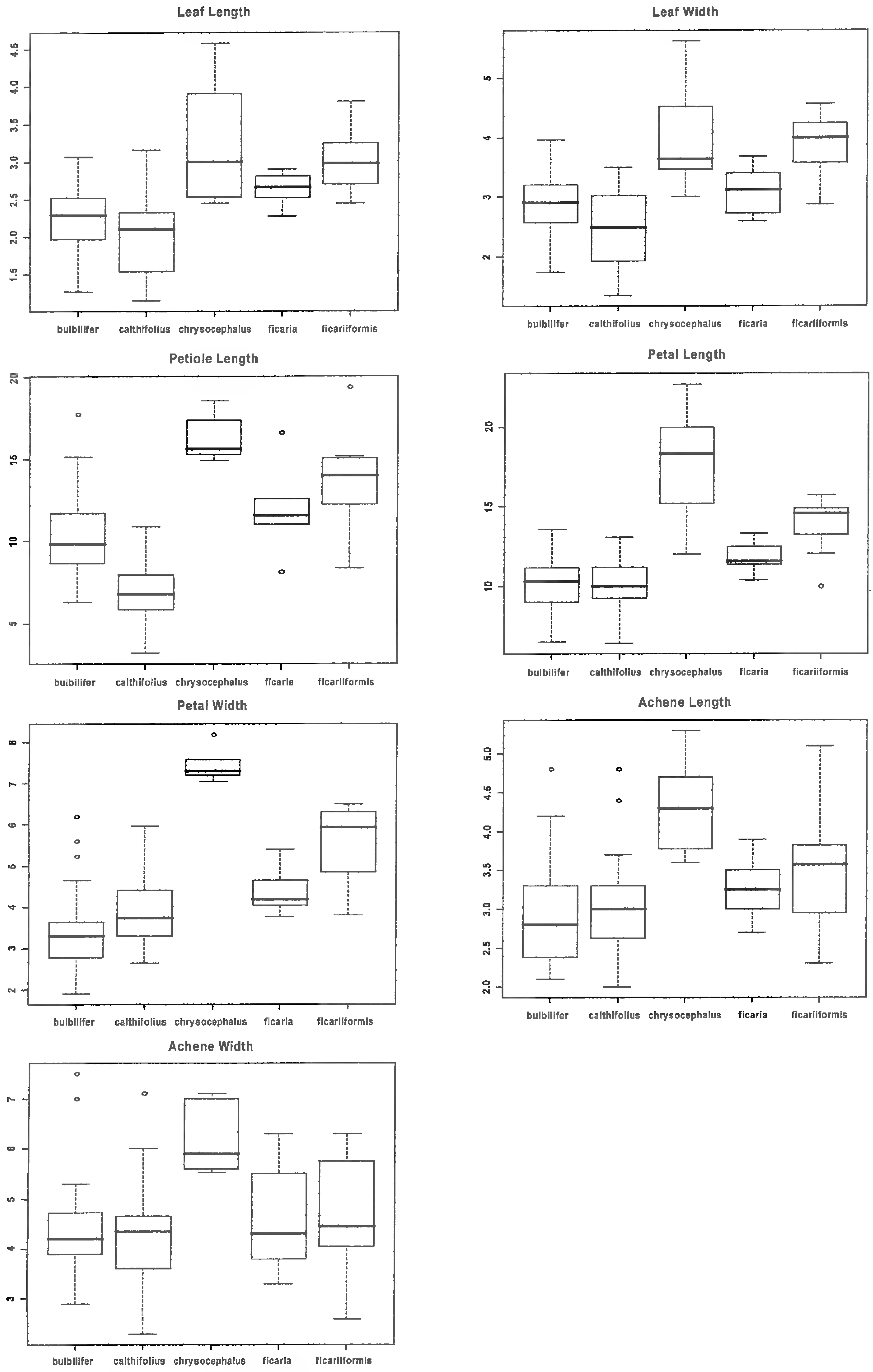

Fig. 1. Boxplots showing distribution of non-transformed measurements for seven quantitative characters in *Ranunculus ficaria* in the United States. Y-axis units are mm, except for leaf characters, which are in cm.

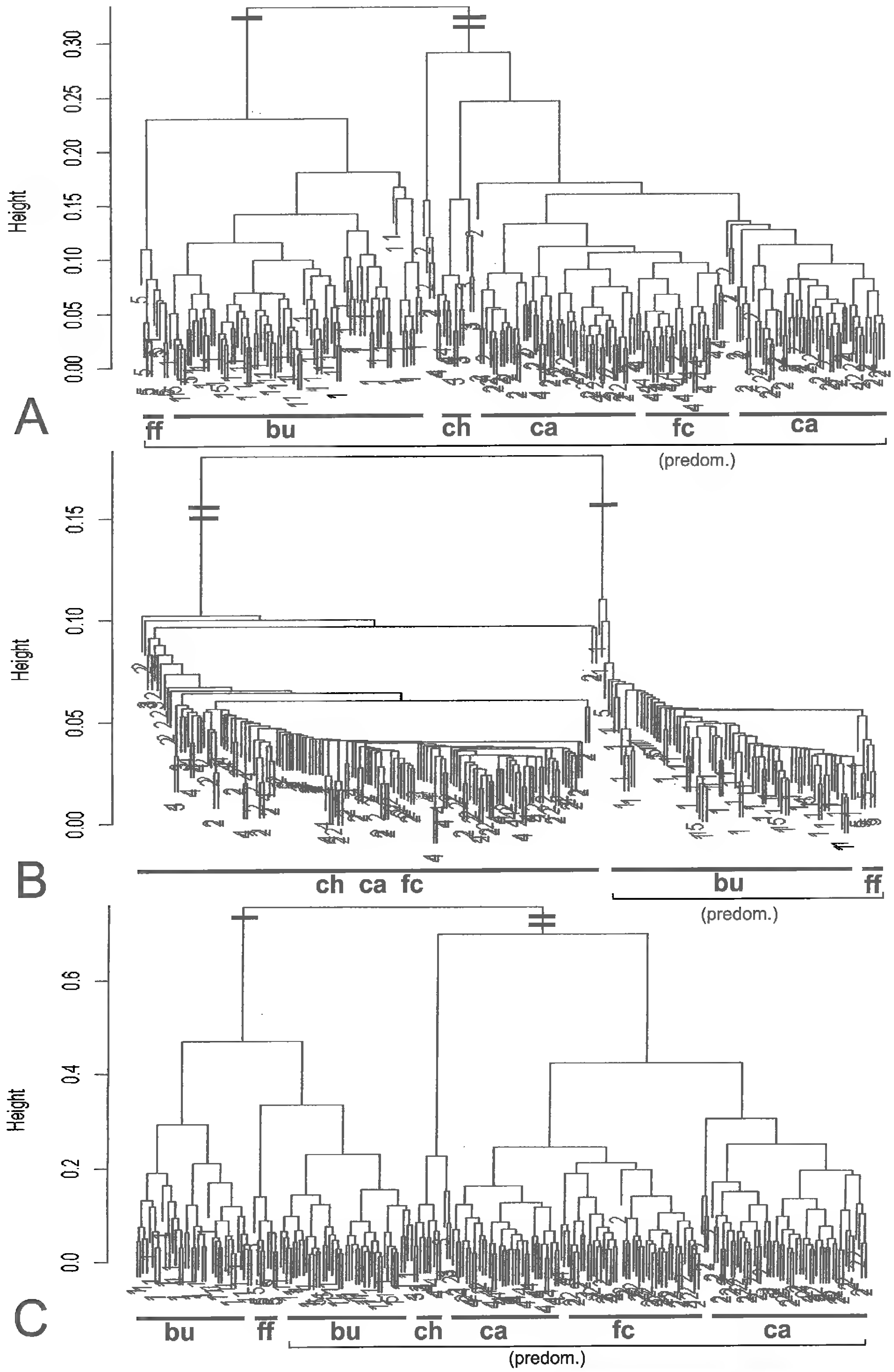

Fig. 2. Cluster analyses of OTUs of *Ranunculus ficaria* in the United States: A, Average linkage (UPGMA); B, Single linkage; C, Complete linkage. Single bar indicates bulbiliferous OTUs. Double bar indicates non-bulbiliferous OTUs. In cases where OTUs sorted incompletely, the predominant taxon in a delineated cluster is indicated followed by "predom." bu = subsp. *bulbilifer* (1); ca = subsp. *calthifolius* (2); ch = subsp. *chrysocephalus* (3); fc = subsp. *ficaria* (4); ff = subsp. *ficariiformis* (5).

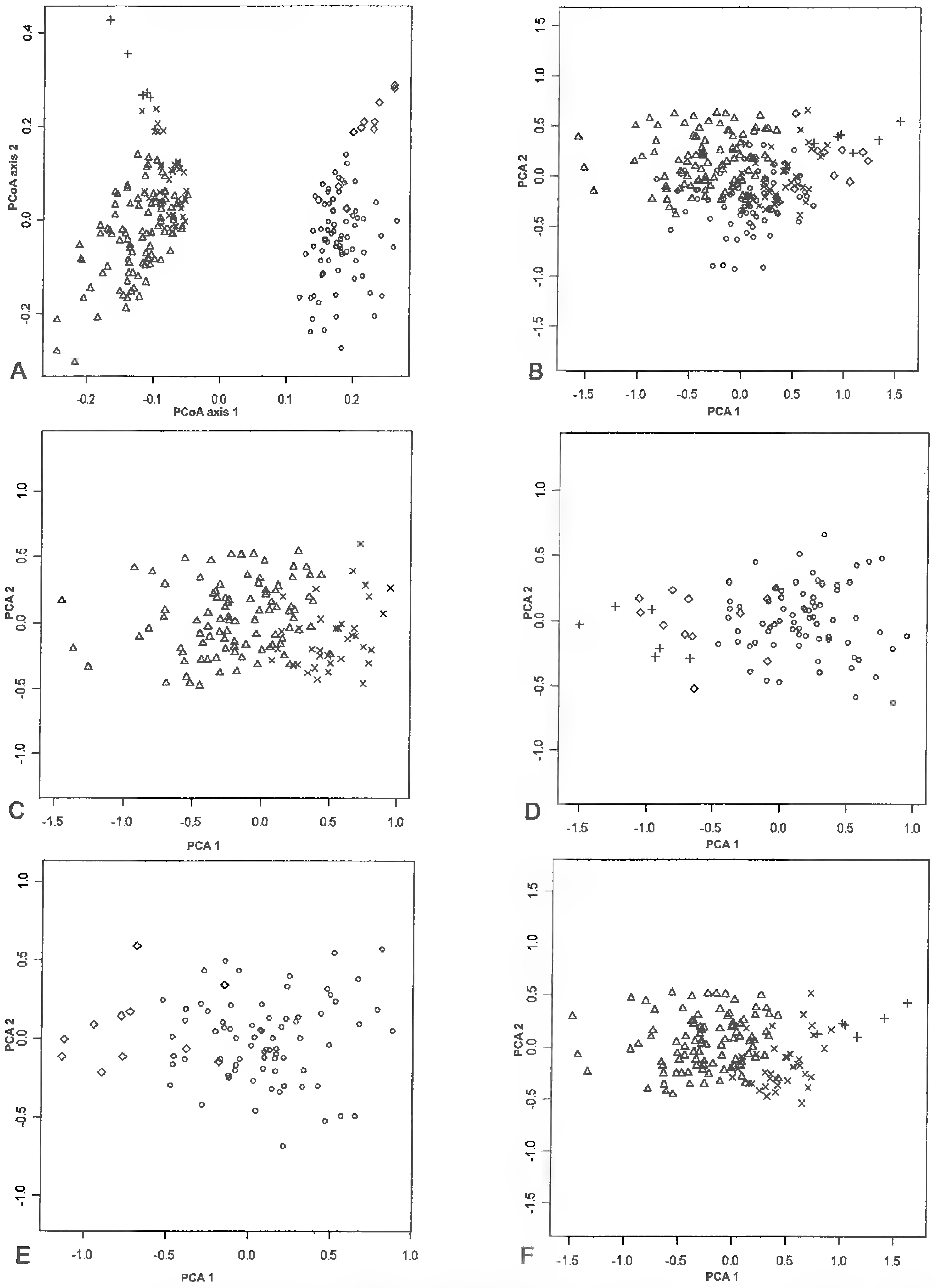

Fig. 3. Ordination results for Principal Coordinates Analysis (A: all OTUs) and Principal Components Analyses (B–F); B: all OTUs; C: putative diploid OTUs; D: putative tetraploid OTUs; E: bulbiliferous OTUs; F: non-bulbiliferous OTUs. o = subsp. *bulbilifer*; Δ = subsp. *calthifolius*; + = subsp. *chrysocephalus*; x = subsp. *ficaria*; ◊ = subsp. *ficariiformis*

Table 2. Character loadings for the first three principal components (PC) in the combined PCA of all OTUs.

	PC1	PC2	PC3
Leaf length	0.4447150	0.06007699	-0.5807531
Leaf width	0.4659988	0.01441147	-0.4945180
Petiole length	0.6942403	-0.45147042	0.5562742
Petal length	0.2116039	0.44013398	0.1484652
Petal width	0.2415118	0.77371804	0.2944399

Table 3. Character loadings for the first three principal components (PC) in the PCA of the putative diploid OTUs.

	PC1	PC2	PC3
Leaf length	0.4393161	0.1933816	-0.5527152
Leaf width	0.4473662	0.1682932	-0.4790156
Petiole length	0.7371736	-0.4948622	0.4585902
Petal length	0.1785614	0.4539478	0.2102479
Petal width	0.1776393	0.6952149	0.4588473

Table 4. Character loadings for the first three principal components (PC) in the PCA of the putative tetraploid OTUs.

	PC1	PC2	PC3
Leaf length	-0.4145495	0.2908487	-0.5513932
Leaf width	-0.4139542	0.2858958	-0.4349598
Petiole length	-0.4282971	0.5777908	0.6924294
Petal length	-0.3705260	-0.3867720	0.1113257
Petal width	-0.5797091	-0.5918072	0.1221624

Table 5. Character loadings for the first three principal components (PC) in the PCA of the bulbiliferous OTUs.

	PC1	PC2	PC3
Leaf length	-0.4166727	-0.2045966	0.5826665
Leaf width	-0.4395120	-0.2045104	0.4630089
Petiole length	-0.4585246	-0.6345035	-0.6193181
Petal length	-0.3303427	0.3747980	-0.1413127
Petal width	-0.5602160	0.6109399	-0.2063936

Table 6. Character loadings for the first three principal components (PC) in the PCA of the non-bulbiliferous OTUs.

	PC1	PC2	PC3
Leaf length	0.4474063	0.1388268	-0.5661383
Leaf width	0.4522951	0.1139208	-0.4887299
Petiole length	0.6954902	-0.5497825	0.4608629
Petal length	0.2280402	0.4510623	0.2216459
Petal width	0.2440242	0.6797288	0.4232127

Seventy-five percent (N=6) and 87.5% (N=7) of OTUs we referred respectively to subsp. *chrysocephalus* and subsp. *ficariiformis* using Sell (1994) could be placed into corresponding homogeneous groups. A quarter of the OTUs (N=2) assigned to subsp. *chrysocephalus* in the analysis were specimens we referred to subsp. *ficaria* using Sell (1994). The presence of bulbils separated the *calthifolius/chrysocephalus/ficaria* group from

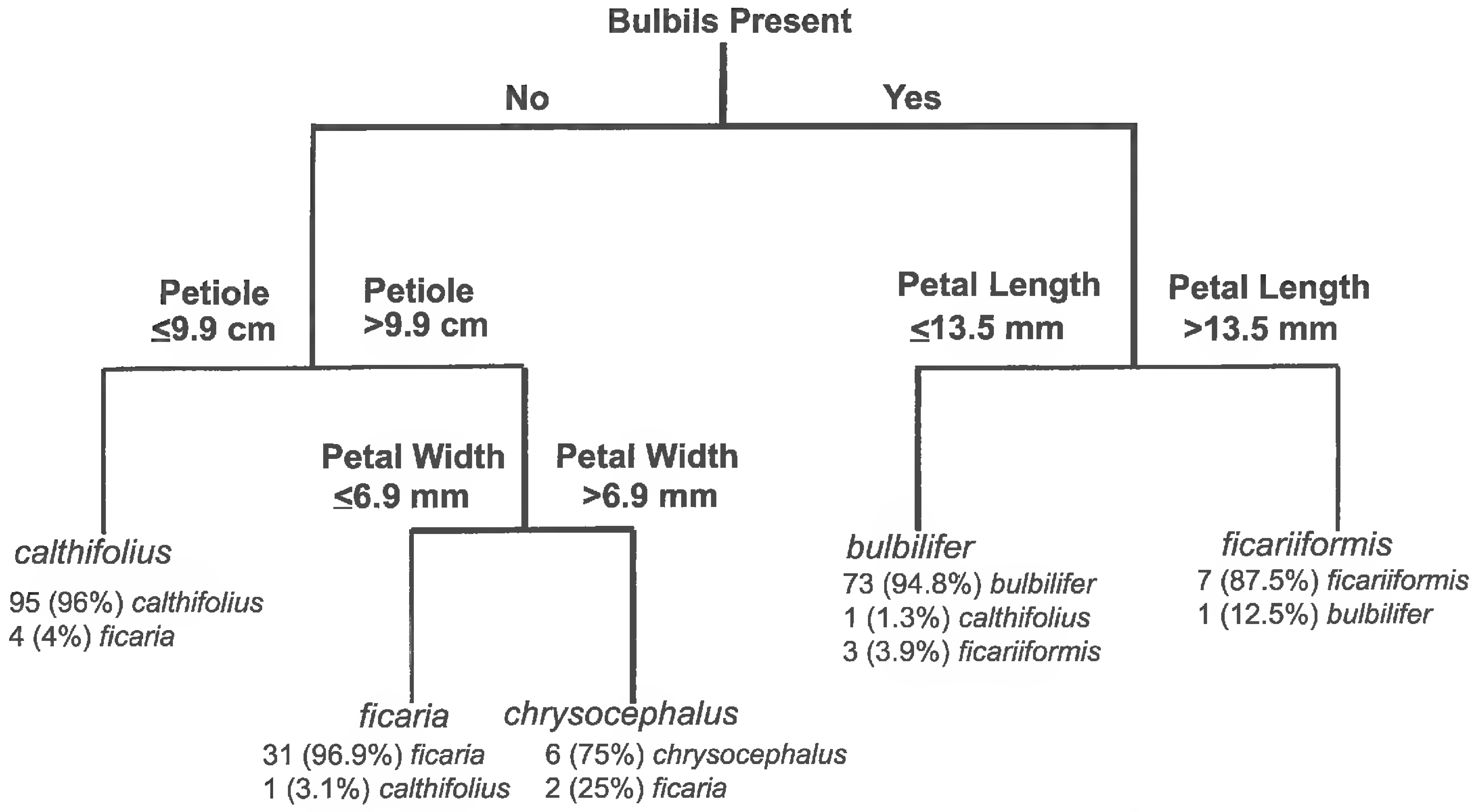

Fig. 4. Classification tree analysis. Numbers given at node terminals indicate our *a priori* classifications sensu Sell (1994). For example, the model assigned ninety-nine OTUs to the *calthifolius* node terminal. Ninety-five OTUs (96%) from this node were assigned to *calthifolius* by us and four (4%) were assigned to *ficaria* by us.

the *bulbilifer/ficariiformis* group. Within the former, petiole length discriminated best between OTUs referable to subsp. *calthifolius* and those referable to subsp. *ficaria* and subsp. *chrysocephalus*. Petal width discriminated best between subsp. *ficaria* and subsp. *chrysocephalus*. Petal length discriminated best between subsp. *bulbilifer* and subsp. *ficariiformis*. The shape of bulbils was not scored for the classification tree analysis as we were interested in seeing what additional vegetative character distinguished these putative taxa.

DISCUSSION

Subspecies recognition.—The combined results indicate the presence of five entities that can be reasonably referred to the subspecies accepted by Sell (1994). If one accepts subspecies as incompletely diverged lineages, one would expect a limited amount of overlap of OTUs as seen in our PCoA and PCA results, as well as incompletely sorted OTUs as seen in our cluster and classification tree analyses (Rosen et al. 2007). The ANOVA results are also informative on this issue, particularly because the assignment of each OTU to a putative subspecies was based exclusively on the key by Sell (1994; see above). In this key, quantitative measurements were used only to distinguish two groups of subspecies (i.e., *chrysocephalus/ficariiformis* and *bulbilifer/calthifolius/ficaria*). *Qualitative* characters are used in Sell's (1994) key to distinguish individual subspecies within these two groups. Thus, contributing evidence of the morphological cohesiveness of the subspecies concept of Sell (1994) is the extent to which differences in quantitative characters are found between all subspecies pairs. Of course, had we found that our OTU groups assigned to the subspecies sensu Sell (1994) did not differ significantly in quantitative characters, it would not necessarily have challenged Sell's concepts, as the taxa may truly differ only in qualitative characters. However, the finding that the OTU groups corresponding to the subspecies sensu Sell (1994) do in fact differ in various combinations of the quantitative characters we examined provides some additional evidence of distinctness. Although the groups differed primarily in the means of quantitative characters and showed overlap in maximum dimensions, if one accepts a subspecies as an incompletely diverged lineage, overlap in character states cannot be

unexpected. In addition, distinct means in quantitative characters could be viewed as a reflection of partial isolation and potentially emerging distinct evolutionary trajectories, possibly leading to speciation. In recognizing that our analysis is limited to plants introduced to the United States, our results could be biased if our data sets largely contained "non-controversial" individuals (e.g., individuals from subspecific centers of distribution in Europe, rather than regions of overlap). There is no way to know this, except through a broader study. However, we did not explicitly seek to test the subspecies concept sensu Sell (1994), but rather whether plants introduced to the United States could be reasonably referred to that concept—which we believe they can. The recognition of subspecies of *R. ficaria* has obvious practical consequences in weed management, as not all subspecies may behave in the same manner.

Summary of taxon distribution, habitat, and rate of spread.—Based on our current understanding, the subspecies of *R. ficaria* exhibit overlapping distributions in the United States (Fig. 5). Subspecies *calthifolius* occurs in eighteen states and the District of Columbia. It was apparently first collected in the United States in 1867 (Pennsylvania: *Burke s.n.*, PH). Collections of this subspecies account for 35.5% of specimens examined. Subspecies *bulbilifer* currently occurs in sixteen states and the District of Columbia. It was apparently first collected in the United States in 1891 (New York: *Hollick s.n*, LGO) and accounts for 31.5% of the specimens examined. Subspecies *ficaria* occurs in ten states and the District of Columbia. It was apparently first collected in the United States in 1876 (New York: *Schrenck s.n.*, LGO) and accounts for 15% of the collections examined. Subspecies *ficariiformis* currently occurs in Missouri, North Carolina, New York, Ohio, Pennsylvania, and Texas. It was apparently first collected in the United States in 1910 (Pennsylvania: *St. John 111*, GH) and accounts for only 8% of specimens examined. Subspecies *chrysocephalus* currently is known only from Maryland, New York, Oregon, and Washington. It was apparently first collected in the United States in 1975 (Oregon: *Hatch s.n.*, NY, OSC). The narrower range documented for subsp. *chrysocephalus* vis-à-vis the other subspecies is attributed to the recency of introduction—collections of this subspecies in the United States are unknown prior to 1975. The disjunct populations in the east and west likely resulted from secondary introductions through the horticultural trade.

All subspecies of *Ranunculus ficaria* are best adapted to moist sites (Taylor & Markham 1978). All perform well in irrigated landscapes, such as lawns and horticultural plantings, but occur in a variety of habitats from moist woods to roadsides and lawns (Fig. 6). The majority of collections of all subspecies (45.9%) were made adjacent to a water source such as a river, stream, or pond. An additional 15.5% came from other moist areas. Collections from lawns and horticultural plantings were equal at 8.13% each. A few specimens have been collected in other habitats such as disturbed sites, lowlands, and fields. Twenty-three percent of specimens of subsp. *ficariiformis* were collected from dry woods suggesting that this subspecies may tolerate more xeric environments than the other four. Habitat distributions of subsp. *chrysocephalus* and subsp. *ficariiformis* likely represent only a limited percent of the habitat range of these taxa due to the limited number of collections they are based upon (N = 6 and N = 13, respectively).

Vegetative spread occurs through tuberous roots, although subsp. *bulbilifer* and subsp. *ficariiformis* also produce axillary bulbils for reproduction (Taylor & Markham 1978; Sell 1994). All subspecies except subsp. *bulbilifer* produce viable seed which frequently fall adjacent to parent plants (Marsden-Jones 1937). Dispersal over long distances likely occurs anthropogenically. The subspecies multiply easily along riverbanks, forming dense mats where there is seasonal flooding (Taylor & Markham 1978). Short distance dispersal is effected by seasonal flood waters which may transport tubers or bulbils downstream. This dispersal pattern was confirmed by primary observation on subsp. *ficariiformis* in Wake Co., North Carolina, in the spring of 2006. The subspecies was distributed along a drainage ditch, through a culvert under the road, and into a local waterway where it colonized banks downstream from the source. Persistence in the landscape is exacerbated by continued use in the nursery trade as a garden plant. Plants may slowly escape from cultivation and spread when tuberous roots, bulbils, or small plants are discarded in yard waste.

Figure 7 shows the relative rate of spread of each subspecies by the number of counties in which it was collected by decade. It does not appear that any single subspecies of *R. ficaria* is more invasive than another

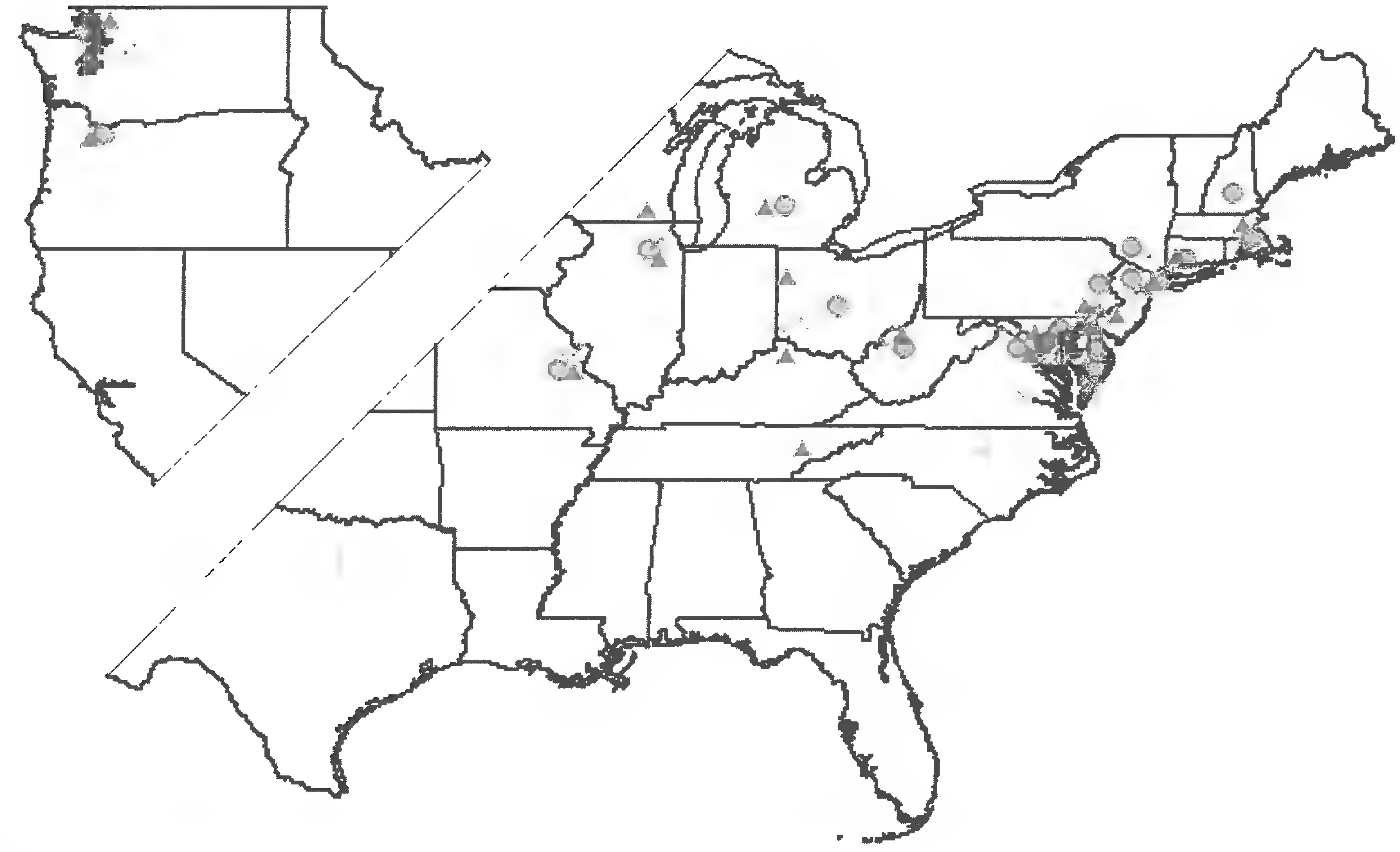

Fig. 5. Distribution of *Ranunculus ficaria* and its five subspecies in the United States as of 2008. ● = subsp. *bulbilifer*; ▲ = subsp. *calthifolius*; + = subsp. *chrysocephalus*; ★ = subsp. *ficaria*; ♦ = subsp. *ficariiformis*.

in the United States. There is no significant difference among the expansion slopes of the five subspecies during the first forty years after each introduction (p=0.0769), suggesting that each subspecies behaves similarly, at least in the early phases of expansion. It may be expected, therefore, that more recently introduced taxa, such as subsp. *chrysocephalus*, subsp. *ficaria*, and subsp. *ficariiformis*, will follow a similar pattern to that of the earlier introductions, subsp. *bulbilifer* and subsp. *calthifolius*, and extend their ranges at similar exponential growth rates in the next hundred years.

All subspecies of *R. ficaria* should be expected to persist where introduced throughout most of Canada, New England to Iowa, possibly northern California, and as far south as Texas. We have not seen collections from California, Iowa, Indiana, Maine, Rhode Island, or Vermont, although expect that subspecies will persist there, as well. The Midwestern states of Arizona, Colorado, Idaho, Kansas, North Dakota, Nebraska, Nevada, Oklahoma, South Dakota, Utah, and Wyoming are likely too arid for widespread naturalization. However, subspecies may establish locally in irrigated areas or wetlands following introduction.

APPENDIX A

List of exsiccatae of *Ranunculus ficaria* in the United States. Arranged alphabetically by subspecies. * = handwriting difficult to decipher; ♣ = double flowers.

Ranunculus ficaria L. subsp. **bulbilifer** Lambinon

U.S.A. CONNECTICUT. New Haven Co.: 12 May 1992, *Mehrhoff 15469* (CONN, Y); 4 Jun 1997, *Morehead III 3561* (CONN). **DELAWARE. New Castle Co.:** 24 Apr 2004, *Clancy 5905* (DOV); Apr 1978, *Lindtner 109* (DOV); *Schuyler 7210* (PH). **DISTRICT OF COLUMBIA:** 27 Apr 1993, *Redman 6651* (BALT). **ILLINOIS. Cook Co.:** 6 May 1987, *Evert 11832* (MOR); 6 May 1987, *Evert 11833* (MOR); 17 May 1989, *Evert 16279* (MOR, NA); 8 May 1997, *Hickman 514* (MOR); 26 May 1978, *Kamin 945-3000* (MOR); 2 May 1982, *Lace s.n.* (MOR); 5 May 1998, *Masi, Epting, & Kossovich 817* (ILLS); 1 May 1960, *Venrick 122* (MO). **Dupage Co.:** 27 Apr 2003, *Kobal FPD03-02* (MOR); 5 May 1995, *Lampa 95-03* (MOR). **Lake Co.:** 27 May 1998, *Fiest 24* (ILLS). **MARYLAND. Baltimore Co.:** 26 Apr 1975, *Beach 0107* (MARY); 17 Apr 1984, *Hill 13552* (BRIT, GH, MARY, MO, MSC, NY-2 sheets, POM); 22 Mar 1989, *Redman 6320* (BALT); 30 Apr 1993, *Redman 6492* (BALT); 14 Apr 1974, *Romeo 41* (MARY). **Howard Co.:** 30 Apr 1965, *Engh s.n.* (BKL, MARY).

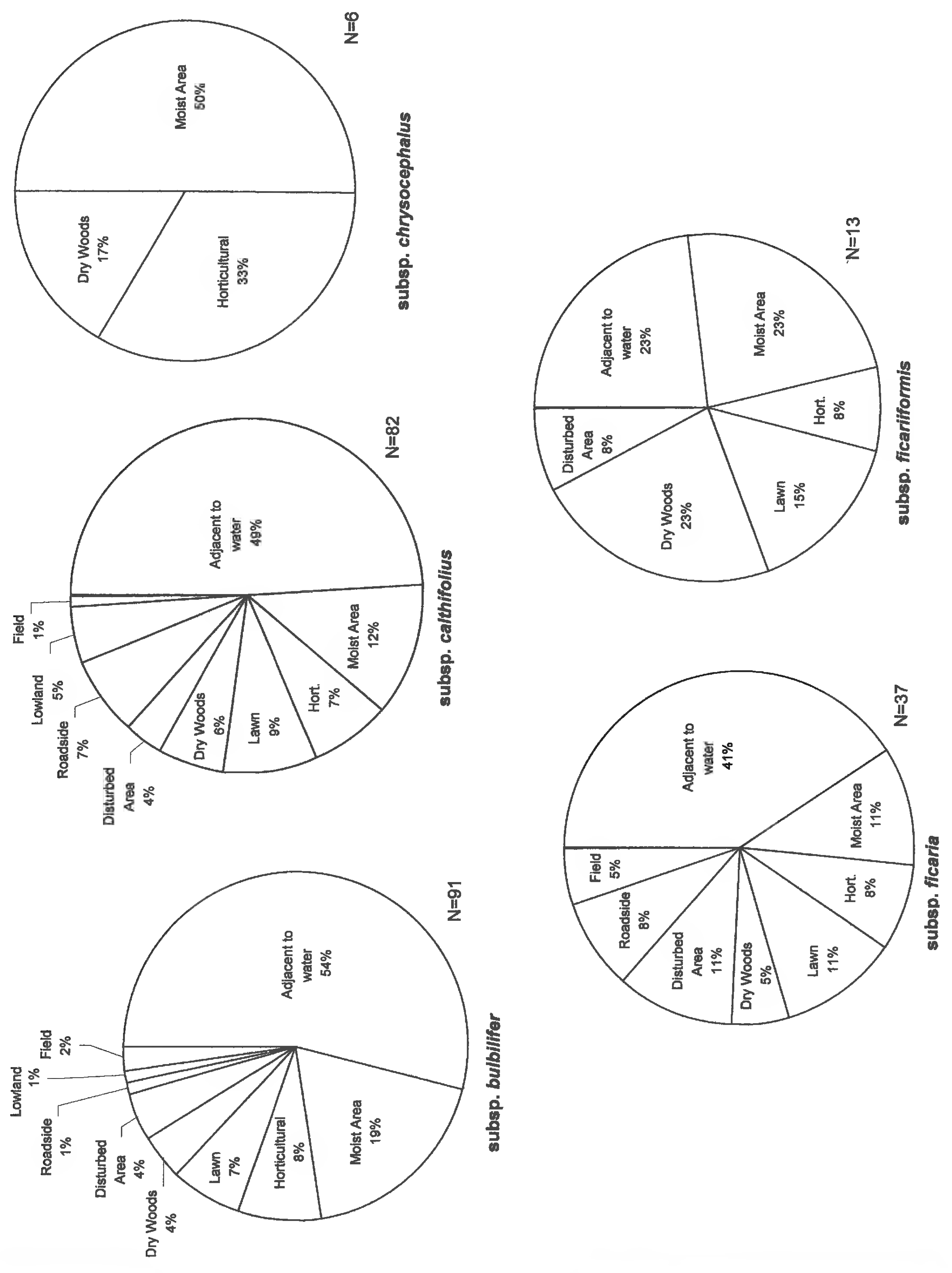

Fig. 6. Percentage of collections from various habitat for each of five subspecies of *Ranunculus ficaria* in the United States.

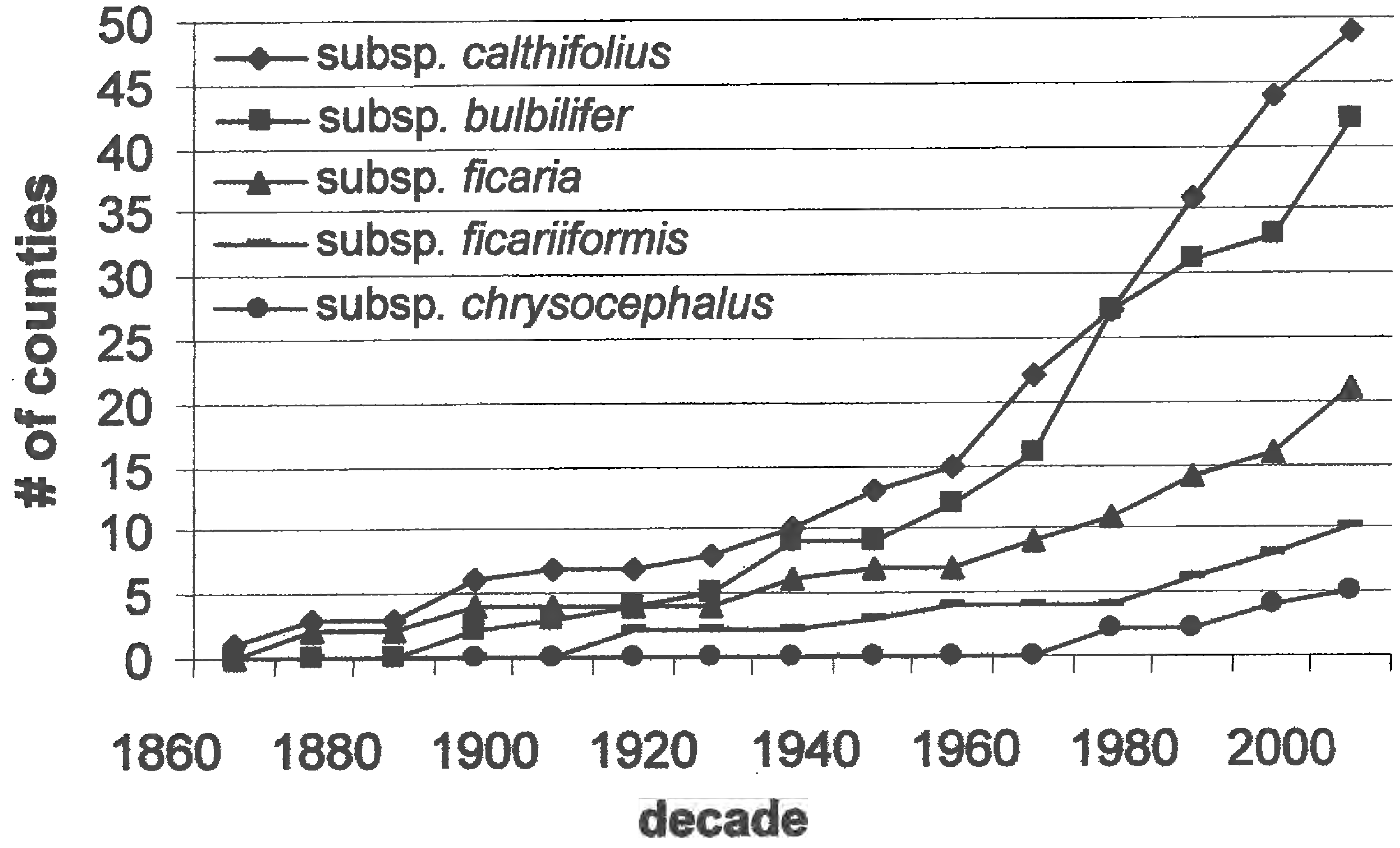

Fig. 7. Rate of spread of each subspecies of *Ranunculus ficaria* based on number of county records per decade. There is no significant difference among the expansion slopes of the five subspecies during the first forty years after each introduction (p = 0.0769).

Montgomery Co.: 25 Apr 1937, *Benedict Jr. 3679* (NA); 18 Apr 1976, *Morris 11* (MARY). **Prince Georges Co.:** 19 Apr 1974, *Bunn 37* (MARY). **MASSACHUSETTS. Suffolk Co.:** 24 May 2004, *Mehrhoff 21169* (CONN). **MICHIGAN. Clinton Co.:** 9 May 1982, *Gereau 966* (MICH, MSC). **Eaton Co.:** 22 May 1984, *Blouch s.n.* (MSC); 31 May 1984, *Blouch s.n.* (MSC). **Ionia Co.:** 21 May 2003, *Reznicek & Kogge 11470* (MICH). **MISSOURI. Saint Louis Co.:** 21 Apr 1985, *Brant 551* (MO); 26 Apr 1972, *Brown s.n.* (MO); 12 Apr 1992, *Ochs 19* (MO). **NEW HAMPSHIRE. Hillsborough Co.:** 13 May 1962, *Stiff s.n.* (NHA). **NEW JERSEY. Essex Co.:** 25 Apr 2003, *Glenn 8181* (BKL). **Hunterdon Co.:** 26 Apr 2001, *Glenn 5425* (BKL). **Mercer Co.:** 22 Apr 2002, *Glenn 8988* (CONN, BKL). **Passaic Co.:** 17 May 1939, *Clausen s.n.* (BH); 6 May 1941, *Langmuir & Lawrence s.n.* (BH). **Somerset Co.:** 23 Apr 2003, *Glenn 8149* (BKL). **NEW YORK. Bronx Co.:** 4 May 1964, *Bennett s.n.* (NY); 28 Apr 1939, *Swift R432/37* (NY); 4 May 1996, *Walker 1868* (NY); 19 Apr 1989, *Yost 355* (DOV). **Cayuga Co.:** 23 May 1932, *Hazard 17883* (CU). **Nassau Co.:** 27 Apr 2001, *Steward 416* (BKL). **Richmond Co.:** 3 May 1937, *Guiler s.n.* (CU); 19 Apr 1891, *Hollick s.n.* (LGO). **Tompkins Co.:** 10 May 1935, *Burnham 18847* (CU); 22 May 1935, *Clausen s.n.* (BH); 22 May 1917, *Gershoy 8104* (CU). **OHIO. Franklin Co.:** 17 Apr 1977, *Carr 68* (OS); 27 Apr 1980, *Carr 2645* (OS); 28 Apr 1987, *Lammers 6084* (OS); 16 Apr 1992, *Lowden 4908* (OS). **Hamilton Co.:** 21 Apr 1982, *Cusick 21469* (OS); 12 Apr 1989, *Cusick 27953* (OS). **Montgomery Co.:** 6 May 1978, *Cusick 18074* (KE, OS); 23 Apr 1998, *McCormac 6484* (MICH). **OREGON. Multnomah Co.:** 26 Apr 1962, *Smith s.n.* (OSC). **PENNSYLVANIA. Berks Co.:** 5 May 1972, *Brumbach 7910* (BH, NA-2 sheets, NY). **Blair Co.:** 1 May 1987, *Kunsman 8564* (PH). **Bucks Co.:** 3 May 1959, *Forman s.n.* (PH); 18 Apr 1998, *Mehrhoff 20039* (CONN). **Chester Co.:** 18 Apr 1959, *Webb & Wherry s.n.* (PH). **Delaware Co.:** 6 Apr 1937, *Blaser s.n.* (CU); 7 May 1944, *Carter 5084* (DOV); Apr 1908, *Painter s.n.* (MO, NA); 16 Apr 1942, *Wheeler 5600* (POM). **LeHigh Co.:** 26 Apr 1959, *Schaeffer Jr. 58388* (PH). **Montgomery Co.:** 22 Apr 1922, *Dreisbach 868* (F, MICH); 24 Apr 1954, *Wherry s.n.* (PH). **Philadelphia Co.:** 26 Apr 1911, *Eckfelds s.n.* (PH-2 sheets); 1 May 1912, *Fackenthall s.n.* (NA); 20 Apr 1911, *St. John s.n.* (GH); 12 Apr 1908, *Van Pelt s.n.* (MICH, PH). **VIRGINIA. Fairfax Co.:** 13 Apr 1976, *Bradley & Frederickson 9954* (WVA). **WASHINGTON. King Co.:** 17 Mar 2002, *Zika & Jacobson 16885* (WTU). **WEST VIRGINIA. Ritchie Co.:** 15 May 1970, *Elliott s.n.* (WVA). **Wood Co.:** 8 Apr 2003, *Grafton s.n.* (WVA).

Ranunculus ficaria L. subsp. **calthifolius** (Reichenb.) Arcangeli

U.S.A. CONNECTICUT. Fairfield Co.: 16 Apr 1985, *Mehrhoff 11192* (CONN). **New Haven Co.:** 20 Apr 2001, *Murray 01-001* (CONN). **Tolland Co.:** 29 Apr 2000, *Mehrhoff 20744* (CONN). **DELAWARE. New Castle Co.:** 4 Apr 1985, *Meyer & Mazzeo 20693* (NA). **DISTRICT OF COLUMBIA:** 20 Mar 1983, *Flemming s.n.* (MARY); 14 Apr 1983, *Fleming s.n.* (NA); 3 Apr 1986, *Fleming 4* (NA); 13 Apr 1899, *Maxon* 72* (NA); ♣ 1874, *McCarthy s.n.* (NA); 26 Apr 1884, *McCarthy s.n.* (NA); 18 Apr 1897, *Topping s.n.* (NA). **ILLINOIS. Cook Co.:** 2 May 1996, *Antonio & Masi 7577* (ILLS); 24 Apr 1966, *Argent M. D. s.n.* (ILLS). **Lake Co.:** 24 Apr 1988, *Snydacker*

561 (F). **KENTUCKY. Campbell Co.:** 12 Apr 1981, *Buddell II 108* (NY). **MARYLAND. Anne Arundel Co.:** 4 Apr 1991, *Longbottom 1460* (MARY); 15 Apr 1993, *Longbottom 3473* (MARY). **Baltimore Co.:** 23 Apr 1971, *Chanoski 043* (BALT); 3 Apr 1980, *Critikos 9* (BALT); 4 Apr 1977, *Lears s.n.* (MARY); 13 Apr 1974, *Ness 33* (MARY); 1 May 1984, *Redman 4029* (BALT). **Caroll Co.:** 13 Apr 1963, *Burroughs 31* (MARY). **Howard Co.:** 17 Apr 1965, *Stolze 386* (F-2 sheets). **Montgomery Co.:** 25 Jan 1950, *Cross s.n.* (NA); 27 Mar 1976, *Mora 22* (MARY); 1 Apr 1971, *Sappington s.n.* (MARY); 6 Apr 1975, *Schlossberg 0002* (MARY); 19 Mar 1983, *Zastrow 1* (OSC). **Prince Georges Co.:** 9 Apr 1987, *Bowman 377* (MARY); 13 Apr 1970, *Thompson Jr. s.n.* (MARY). **MASSACHUSETTS. Middlesex Co.:** 8 May 1982, *Wood 4690* (MT). **MICHIGAN. Ionia Co.:** 23 Apr 1989, *Penskar 1085* (MICH); 24 Apr 1989, *Penskar 1086* (MICH). **MISSOURI. Saint Louis Co.:** 4 Apr 1989, *Yatskievych, Yatskievych, Denison 89-05* (MO); 1 Apr 1999, *Yatskievych, Yatskievych, Harris, Harris, & Summers 99-04* (MO). **NEW JERSEY. Burlington Co.:** 16 Apr 1932, *Stokes M.D. s.n.* (PH). **Camden Co.:** 23 Apr 1898, *Saunders s.n.* (PH). **Middlesex Co.:** 12 Apr 2003, *Martine & Skogen 354* (CONN). **Somerset Co.:** 7 Apr 2000, *Glenn 4065* (BKL). **Union Co.:** 3 Apr 2002, *Glenn & Steward 6197* (BKL). **NEW YORK. Bronx Co.:** 11 Apr 1976, *Delendick s.n.* (BKL). **Dutchess Co.:** May 1941, *Van Melle s.n.* (BH). **Queens Co.:** Apr 1876, *Schrenk s.n.* (LGO); 1876, *Schrenk s.n.* (LGO); 25 Apr 1877, *Schrenk s.n.* (BKL, MO); Apr 1877, *Schrenk s.n.* (PH); 11 Apr 1878, *Schrenk s.n.* (MICH); Apr 1878, *Schrenk s.n.* (BKL, F-2 sheets, HNH, NA, NY-2 sheets, POM); Apr 1878, *Schrenk s.n.* (LGO-2 sheets, NA); May 1882, *Bisky s.n.* (BKL). **Richmond Co.:** 13 Apr 1898, *Coheu* s.n.* (BKL-2 sheets). **Tompkins Co.:** 7 May 1937, *Anderson s.n.* (MASS); ♣19 Apr 1959, *Dress 5984* (BH); 1 May 1996, *Dress 19996* (BH). **OHIO. Clark Co.:** 31 Mar 1992, *Cusick 30056* (OS). **Clermont Co.:** 2 Apr 1996, *Cusick 32886* (MO, OS). **Clinton Co.:** 3 Apr 1989, *Cusick 27946* (OS). **Franklin Co.:** 5 Apr 1986, *Cooperband 5* (OS); 29 Mar 1987, *Cusick 26207* (NY). **Greene Co.:** 31 Mar 1992, *Cusick 30054* (OS). **Lake Co.:** 2 Jun 1901, *Hacker s.n.* (OS). **Van Wert Co.:** 22 Apr 1946, *Brooks 1393* (OS); 28 Apr 1947, *Brooks s.n.* (OS). **OREGON. Multnomah Co.:** 27 Mar 1991, *Zika 11064* (OSC). **PENNSYLVANIA. Bucks Co.:** 18 Apr 1962, *Wherry s.n.* (PH). **Delaware Co.:** 13 Apr 1934, *Fogg Jr. 6316* (PH); 12 Apr 1938, *Fogg Jr. 14021* (GH); 7 Apr 1894, *MacElwee Jr. s.n.* (PH); 12 Apr 1920, *Meredith M.D. s.n.* (NY); 15 Apr 1942, *Schaeffer Jr. 16953* (PH-2 sheets); 19 Apr 1936, *Thompson Jr. 17* (PH); **Greene Co.:** 4 Apr 1953, *Buker s.n.* (PH). **Montgomery Co.:** ♣19 Apr 1963, *Fogg Jr. 22220* (A); 3 Apr 1921, *Long 23784* (PH); 20 Apr 1937, *Long 49720* (PH); 18 Feb 1954, *Long 77721* (PH); 1 May 1985, *Weaver s.n.* (PH). **Philadelphia Co.:** ♣1867, *Burke s.n.* (PH); ♣10 Apr 1954, *Fogg Jr. 21460* (PH-2 sheets); ♣18 Apr 1954, *Fogg Jr. 21474* (PH); 3 Apr 1933, *Hermann 3953* (NA); 18 Apr 1974, *Jers** (PH); ♣27 Apr 1924, *Lang 112* (GH); ♣1 May 1920, *Meredith M.D.* (NY); 30 Mar 1909, *St. John 110* (GH). **TENNESSEE. Knox Co.:** 17 Mar 1977, *DeSelm s.n.* (TENN); 25 Mar 1966, *Thomas s.n.* (BRIT); 31 Mar 1966, *Thomas & Rogers s.n.* (TENN). **VIRGINIA. Albemarle Co.:** 25 Mar 1997, *Stevens 25629* (VPI). **Chester Co.:** 3 Apr 1999, *Huber 1* (ILLS, OS). **Fairfax Co.:** 13 Apr 1947, *Sargent s.n.* (NCSC); 23 Mar 1974, *Sperling 36* (MARY). **WASHINGTON. Whatcom Co.:** 5 Apr 1968, *Sundquist 1550* (POM). **WEST VIRGINIA. Ritchie Co.:** 15 Apr 1963, *Stonestreet s.n.* (WVA). **WISCONSIN. Walworth Co.:** May 1970, *Larkin s.n.* (MOR).

Ranunculus ficaria L. subsp. **chrysocephalus** P.D. Sell
U.S.A. MARYLAND. Prince Georges Co.: 27 Mar 1977, *Wirick 05* (MARY). **NEW YORK. Tompkins Co.:** 18 May 1996, *Dress 15977* (CU). **OREGON. Benton Co.:** 31 Mar 1991, *Zika 11065* (OSC). **Lane Co.:** 22 Feb 1975, *Hatch s.n.* (NY, OSC). **WASHINGTON. King Co.:** 17 May 2002, *Zika & Jacobson 13733* (WTU).

Ranunculus ficaria L. subsp. **ficaria**
U.S.A. DISTRICT OF COLUMBIA: ♣ 29 Apr 1896, *Pollard 776* (NY); ♣29 Apr 1896, *Pollard 776* (MSC); ♣29 Apr 1896, *Pollard s.n.* (POM); ♣17 Apr 1898, *Pollard s.n.* (NY); ♣17 Apr 1898, *Steele s.n.* (MSC); ♣18 Apr 1897, *Steele s.n.* (GH); ♣ 18 Apr 1897, *Steele s.n.* (NA); ♣18 Apr 1897, *Steele s.n.* (NY). **ILLINOIS. Lake Co.:** 24 Apr 1988, *Snydacker 560* (MOR). **MARYLAND. Baltimore Co.:** 13 Apr 1980, *Caruso 22* (BALT); 5 Apr 1980, *King 10* (MARY). **Howard Co.:** 25 Mar 1989, *Redman 6321* (BALT). **Montgomery Co.:** 19 Apr 1975, *Hollenberg 8* (MARY); 19 Apr 1979, *Trumball 4* (BRIT); 13 Apr 1975, *Yinger 17* (MOR). **Prince Georges Co.:** 10 Apr 1977, *Dochtermann 29* (MARY); 16 Apr 1994, *Hedge 13* (MARY); 2 Apr 1982, *Kunowsky 10* (MARY); 4 Apr 1964, *Weigel Jr. s.n.* (MARY). **MASSACHUSETTS. Hampshire Co.:** 24 Apr 2002, *Mehrhoff 21611* (CONN, MASS). **MISSOURI. Saint Louis Co.:** 11 Apr 1990, *Christ s.n.* (MO); **NEW JERSEY. Mercer Co.:** 18 Apr 2001, *Glenn 5386* (BKL). **Somerset Co.:** 19 Apr 2001, *Glenn 5401* (BKL). **NEW YORK. Cayuga Co.:** 7 Jun 1935, *Petry 18846* (CU). **Dutchess Co.:** 1932, *Van Melle s.n.* (BH). **Queens Co.:** 22 Apr 1990, *Greller s.n.* (BKL); 1921, *Martin s.n.* (PH); Apr 1877, *Redfield 10896* (MO); Apr 1876, *Schrenk s.n.* (LGO). **OHIO. Butler Co.:** 2 Apr 1997, *Turner 31* (MU). **PENNSYLVANIA. Chester Co.:** ♣22 Apr 1941, *Terrell Jr. 375* (PH); ♣6 May 1954, *Wherry s.n.* (PH). **Delaware Co.:** 30 Apr 1892, *Brinton M. D.* (PH-3 sheets); Apr 1903, *Conard s.n.* (PH); 5 Apr 1935, *Fogg Jr. 7996* (PH); 1 May 1904, *Jahn s.n.* (PH); 4 Apr 1946, *Proctor 1716* (NHA). **Northampton Co.:** 2 May 1969, *Tucker s.n.* (DOV). **Philadelphia Co.:** ♣20 Apr 1921, *Henslow s.n.* (PH); ♣23 Apr 1932, *Hermann 2752* (NA); ♣May 1878, *Martindale s.n.* (NA, LGO); ♣12 May 1904, *Van Pelt s.n.* (PH). **WASHINGTON. King Co.:** 8 Mar 2000, *Zika & Jacobson 14827* (WTU). **WEST VIRGINIA. Wood Co.:** 12 Apr 2003, *Grafton s.n.* (WVA).

Ranunculus ficaria L. subsp. **ficariiformis** (F.W. Schwartz) Rouy & Fouc
U.S.A. MISSOURI. Saint Louis Co.: 19 May 1994, *Ladd 18515* (MO). **NEW YORK. Bronx Co.:** 17 Apr 1988, *Mori & Gracie 18815* (GH, MO, NY). **Nassau Co.:** 8 May 1950, *Abbott s.n.* (CU). **Suffolk Co.:** 1 May 2003, *Glenn 8215* (BKL). **Westchester Co.:** 2 May 1994, *Walker 684* (NY). **NORTH CAROLINA. Wake Co.:** 11 Apr 2005, *Krings 1271* (AUA, F, FLAS, GA, LSU, MISS, NCSC-2 sheets, NCU, TEX, UNA, US, USF, USCH, VDB). **OHIO. Butler Co.:** 5 Apr 1988, *Cusick 27224* (OS). **PENNSYLVANIA. Delaware Co.:** 16 May

1915, *Cramfondi* s.n.* (PH); 26 May 1920, *Long 23006* (PH). **Philadelphia Co.:** 7 May 1910, *St. John 111* (GH). **TEXAS. Tarrant Co.:** 8 Mar 2008, *Nesom FW08-1* (NCSC).

Ranunculus ficaria L. (subspecific determination not feasible)
U.S.A. CONNETICUT. Middlesex Co.: 27 Apr 1991, *Swan s.n.* (Y). **New Haven Co.:** 18 Apr 1995, *Brown 1* (Y); 10 May 1993, *Souther s.n.* (Y). **MARYLAND. Baltimore Co.:** 25 Apr 1948, *Moudry s.n.* (MARY); 21 Apr 1968, *Redman s.n.* (BALT). **Howard Co.:** 17 Apr 1966, *Engh s.n.* (MARY). **Prince Georges Co.:** 19 Apr 1979, *Mills Jr. 14* (BRIT). **MASSACHUSETTS. Barnstable Co.:** 27 Apr 2001, *Mehrhoff 21129* (CONN). **MICHIGAN. Ingham Co.:** 10 Apr 1991, *Stephenson s.n.* (MSC). **NEW JERSEY. Union Co.:** 3 Apr 1977, *Moldenke & Moldenke 31285* (NY); 10 May 1978, *Moldenke & Moldenke 31642* (NY). **NEW YORK. Nassau Co.:** 4 May 2004, *Bennett 030031* (BKL). **Queens Co.:** 27 Apr 1918, *Ferguson 7* (NY); 17 Apr 1921, *Martin s.n.* (NY); 30 Apr 1876, *Schrenck s.n.* (CU). **OHIO. MONTGOMERY Co.:** 18 Mar 1990, *McCormac 1977* (MICH, OS). **OREGON. Multnomah Co.:** 4 Apr 1991, *Zika 11066* (OSC). **PENNSYLVANIA. Chester Co.:** 15 Apr 1957, *Wilkens 9129* (PH). **Delaware Co.:** 7 May 1977, *Brown 199* (Y); 24 Apr 1894, *MacElwee Jr. s.n.* (PH). **Philadelphia Co.:** 11 Apr 1954, *Fogg Jr. 21461* (PH). **WEST VIRGINIA. Monongalia Co.:** 12 Apr 1995, *Baer s.n.* (WVA). **Ritchie Co.:** 25 Apr 1971, *Elliott s.n.* (WVA); 27 Apr 1991, *Grafton s.n.* (WVA).

ACKNOWLEDGMENTS

We thank the following herbaria and their staff for making specimens available to us for study: A, AUA, BALT, BH, BKL, BRIT, CONN, CU, DOV, F, FLAS, GA, GH, HNH, ILLS, KE, LGO, LSU, MARY, MASS, MICH, MISS, MO, MOR, MSC, MT, MU, NA, NCSC, NCU, NHA, NY, OS, OSC, PH, POM, TENN, TEX, UNA, US, USF, USCH, VDB, VPI, WTU, WVA, Y. We also thank David Schuman and Steve Stanislav for statistical support. Three anonymous reviewers offered constructive comments on an earlier draft of the ms.

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BOOK REVIEW

William A. Weber and Ronald C. Wittmann. 2007. **Bryophytes of Colorado: Mosses, Liverworts, and Hornworts.** (ISBN 978-0979090912, pbk.). Pilgrims Process, Inc., P.O. Box 32597, Santa Fe, New Mexico 87594-2597, U.S.A. (**Orders:** www.pilgrimsprocess.com, 1-720-937-6641). $29.95, 231 pp., 8 1/2" × 11".

Almost too small to appreciate except *en masse*, bryophytes are not simple. When viewed with a hand lens or microscope some of the most interesting, unusual, and captivating structures in the plant world are revealed.

The genesis for the current work began with a preliminary publication by Weber in 1973. He presented a catalog and keys of the mosses, at that time identifying about 290 species without including liverworts and hornworts. The current work describes over 500 species including the liverworts and hornworts and is the most comprehensive study of Colorado mosses and liverworts to date. It will be useful in adjacent parts of neighboring states and in the mountainous regions of the interior western United States.

Beginners and students will find this book a valuable reference even though it does not have complete descriptions. Keys to the genera and species are combined with notes on recognition in the field. The authors concentrate on distinguishing characteristics of similar taxa and providing comprehensive ecological notes. Keys are furnished for the identification of genera and species, but the authors have been unable to produce a useful key to the families. They note that there are family keys available on the internet, but that for the seasoned bryologist, family identification is a matter of experience and that for the beginner there is no substitute for a mentor.

Only a few interesting species are illustrated. Readers are referred to the internet for further illustrations of genera and species as well as basic information about their life history and anatomy.

Recommended for the knowledgeable botanist and researcher. Should be available in major collections and research facilities.

William A. Weber is Professor Emeritus at the University of Colorado at Boulder, and the former curator of the University of Colorado Museum Herbarium. He is the author of numerous books on flowering plants, ferns, and lichens as well as bryophytes, concentrating on Colorado and the Rocky Mountains, but international in scope as well.

Ronald C. Wittmann is a professional physicist, an accomplished amateur botanist, and is the co-author of the latest versions of the Colorado Flora.—*Gary L. Jennings, Librarian, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

THE TYPES OF *ASTRAGALUS* SECTION *DIPHYSI* (FABACEAE), A COMPLEX ENDEMIC TO WESTERN NORTH AMERICA, PART I: LECTOTYPIFICATIONS, EPITYPIFICATIONS, AND NEW COMBINATIONS OF SEVERAL TAXA

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RESUMEN

This is the first of several papers discussing typification issues found during studies leading to a monograph of *Astragalus* L. Section *Diphysi* A. Gray. A lectotype and an epitype are designated for *A. lentiginosus* Douglas ex Hook. Original material designated here as the holotype of *Astragalus diphysus* A. Gray var. *albiflorus* A. Gray [=*Astragalus lentiginosus* var. *albiflorus* (A. Gray) Schoener] was rediscovered at GH and the status of its priority over the more commonly used name, *A. lentiginosus* var. *diphysus* (A. Gray) M.E. Jones, is discussed. Epitypes are designated for *A. lentiginosus* var. *micans* Barneby and *A. lentiginosus* var. *oropedii* Barneby. Three new combinations, previously recognized as species, are proposed: **A. lentiginosus** var. **bryantii** (Barneby) J.A. Alexander, **A. lentiginosus** var. **iodanthus** (S. Watson) J.A. Alexander, and **A. lentiginosus** var. **pseudiodanthus** (Barneby) J.A. Alexander.

RESUMEN

Este es el primero de varios documentos que discute problemas de tipificación detectados durante los estudios para una monografía de *Astragalus* L. Section *Diphysi* A. Gray. Se designa un lectotipo y epitipo para *A. lentiginosus* Douglas ex Hook. El material original designado aquí como holotipo de *Astragalus diphysus* A. Gray var. *albiflorus* A. Gray [=*Astragalus lentiginosus* var. *albiflorus* (A. Gray) Schoener] fue redescubierto en GH y se discute su prioridad sobre el uso más común del nombre, *A. lentiginosus* var. *diphysus* (A. Gray) M.E. Jones. Son designados epitipos de *A. lentiginosus* var. *micans* Barneby y *A. lentiginosus* var. *oropedii* Barneby. Se proponen tres nuevas combinaciones, previamente reconocidas como especies: **A. lentiginosus** var. **bryantii** (Barneby) J.A. Alexander, **A. lentiginosus** var. **iodanthus** (S. Watson) J.A. Alexander, y **A. lentiginosus** var. **pseudiodanthus** (Barneby) J.A. Alexander.

INTRODUCTION

Astragalus L. Section *Diphysi* A. Gray, a section native to Western North America, is a problematic species complex composed of taxa that were originally described as or have been split as species in the past 150 years. *Astragalus lentiginosus* Douglas ex Hook. (in Hooker 1831) and *A. diphysus* A. Gray (in Gray 1849) were the core species of Section *Diphysi* in the first comprehensive monograph of *Astragalus* by Asa Gray (1863). Sereno Watson (1871) expanded Gray's concept of Section *Diphysi* to include *A. coulteri* Benth. and *A. platytropis* A. Gray, both of which have inflated pods similar to *A. lentiginosus*. Gray's monograph (1863) and Watson's (1871) revision were the primary references for *Astragalus* taxonomy until Marcus E. Jones began publication of treatments in the genus in the late 1890s.

In his 1898 publication, Jones proposed that species from Gray's (1863) Section *Diphysi* should be combined, as varieties, into a greatly expanded concept of *A. lentiginosus*. His full treatment of these species was not widely known until he published his *Revision of North-American Species of Astragalus* in 1923 (Barneby 1964). Jones was a field botanist of unmatched experience. As a taxonomist, he had a disdain for rules of priority and nomenclature, and was known for his often frustrating brevity. Barneby (1945) found "that many of his names covered unreasonable extremes of variation, or that his descriptions and indications of range were either inaccurate or actually misleading" (p.65). Barneby was able to decipher Jones' species only after extensive study of his annotations and vouchers at POM and duplicates at other herbaria (see discussion of *A lancearius* A. Gray and *A. episcopus* S. Watson, Barneby 1964, p. 267; compare descriptions of varieties of *A. lentiginosus* of Jones 1923, p.124–125 and Barneby 1945, p. 65–152; and discussion of the taxonomic

confusion between Jones' species and hybrids which are now synonyms of *A. argophyllus* Nutt. var. *martinii* M.E. Jones, *A. marianus* Barneby, and *A. desereticus* M.E. Jones, Barneby 1964 p.629–635).

Concurrently, Rydberg (1929) delimited all members of Section *Diphysi* as separate species of the genus *Cystium* Steven. Rydberg appeared to have an idealized concept of each of his species. He regularly composed his morphological descriptions and keys from features exclusively on a single type. As a result, his keys and descriptions sometimes did not match the morphology on all specimens he annotated for his monograph. Despite this, Rydberg for his time was more precise than all previous workers in the genus (Barneby 1964).

Barneby (1945) was the first to comprehensively evaluate Jones' and Rydberg's monographs and found that only one overall classification scheme fit the taxa related to *A. lentiginosus* well: the delimitations of all former species into varieties. Barneby's (1945) treatment and his later Monograph (1964) still serve as a precise baseline from which all taxonomic treatments in this group are based.

Different taxonomic interpretations of the degree of morphological differentiation among the many widespread, sympatric, and geographically isolated taxa within this complex have been the major source of disagreement between the revisions of Rydberg (1929), Jones (1923), Barneby (1964, 1989), Isely (1998), and Welsh (2007). Ultimately the major differences in varietal delimitations between these workers stem from their individual interpretation of type specimens and selection of morphological characters representing the nomenclaturally "typical" variant. Despite Barneby's decades of work in sorting out the typification issues leading up to his Monograph, it is still difficult to determine which variant is nomenclaturally "typical" due to the often poor quality of the type material. Barneby compensated for the poor nature of many types by examining specimens from the vicinity of the type locality. The characters found on those specimens became the informal basis for his concept of the nomenclaturally typical variant and the resulting morphological descriptions.

The most recent monographs, Isely (1998) and Welsh (2007), have made significant additions to the knowledge of taxonomic boundaries in this section, but each has added their own entangled varietal delimitations. However, both still use Barneby (1964) as a nomenclatural foundation. For a monograph of the section that is more comprehensive and thorough than Barneby's, nomenclatural issues that have resulted in conflicting varietal delimitations between the major monographs must be resolved. Fortunately, there are more formal processes in use today that seek refine the delimitation of taxa with problematic types. The Linnaean Plant Name Typification Project (<http://www.nhm.ac.uk/research-curation/research /projects/ linnaean-typification/>) has been the forerunner in using modern additions to the lectotypification, epitypification and neotypification articles in the International Code (McNeill et al. 2006). Using the procedures and philosophy of Vander Kloet (1989), Turland and Jarvis (1997), and Krings (2008) as models, this treatment is the first a series of papers proposing new combinations, lectotypifications and epitypifications within Section *Diphysi*. Due to the varietal and nomenclatural complexity of Section Diphysi, a series of papers instead of a single, expansive treatment is necessary. The goal is to stabilize and refine the nomenclature in this group, which will enable the creation of a more comprehensive and less problematic taxonomic revision of this morphologically and taxonomically difficult section.

METHODS

Herbarium specimens were examined at UC in December of 1999, GH in August of 2002, and NY in October of 2003. Additional herbarium specimens were obtained on loan from CAS, DS, K, POM, RM, and RSA. In addition to loans, research was conducted from 2002 to 2008 using the following online type specimen databases: Consortium of California Herbaria Specimen Databases (CAS, DS, JEPS, RSA, SD, UC, UCR, UCSB), University and Jepson Herbaria (2008b); Index of Botanical Specimens (GH), Harvard University Herbaria (2008); Type specimens at the Herbaria (JEPS, UC), University and Jepson Herbaria (2008b); Kew Herbarium Catalogue (K), Royal Botanic Gardens, Kew (2008); Tropicos (MO), Missouri Botanical Garden (2008); The C.V. Starr Virtual Herbarium (NY), New York Botanical Garden (2008); Type Specimen Register

(US), United States National Herbarium (2008). Though the International Code of Botanical Nomenclature (McNeill et al. 2006) was the basis for all nomenclatural decisions, many papers resulting from The Linnaean Plant Name Typification Project (<http://www.nhm.ac.uk/research-curation/research /projects/linnaean-typification/>) were examined for examples of specific applications of the Code. Other typification papers, especially those resulting from the various tropical flora projects, were also examined. Turland and Jarvis (1997) and Krings (2008) were most frequently consulted for example typifications. Vander Kloet (1989) was consulted to determine how other Douglas taxa described by Hooker were lectotypified (i.e., *Vaccinium membranaceum* Douglas ex Hook., p.133).

RESULTS

Astragalus lentiginosus Douglas ex Hook., Fl. Bor.-Amer. 1:151. 1831. *Tragacantha lentiginosa* (Douglas ex Hook.) Kuntze, Revisio Gen. Pl. 2:946. 1891. *Phaca lentiginosa* (Douglas ex Hook.) Piper, Contr. U.S. Natl. Herb. 11:368. 1906. *Cystium lentiginosum* (Douglas ex Hook.) Rydb. Bull. Torrey Bot. Club 40:50. 1913. Protologue: "subalpine ranges of the Blue Mountains of North West America. Douglas." Type: [U.S.A. Oregon]: in the valley of the Blue Mountains near the source of the Wallawallah [Walla Walla] and Utala [Umatilla] Rivers, [no date], *David Douglas s.n.* (lectotype [first step] designated by Barneby 1964: K; lectotype [second step], designated here: K 264018!, the smaller, fruiting, single stemmed element on the upper left hand side of the sheet including the fragment envelope mounted to the right); [U.S.A. Oregon]: on the banks of streams on the southern branches of the Columbia [possibly collected at the same locality as the lectotype], [no date], *David Douglas s.n.* (epitype, designated here: K 264945!, the mostly flowering, larger specimen mounted in the center of the sheet).

Notes.—At K, there are three different specimen sheets filed as types of *Astragalus lentiginosus,* and all of them are mounted with specimens of various species of *Astragalus*. It is not immediately clear which fragments of these specimens are part of the Douglas types. As with other Douglas specimens described as new species by Hooker (1831), none of the type specimens have a locality that matches the location mentioned in the protologue and none have collection numbers.

From an examination of the annotations on the three type sheets, Asa Gray in 1868 was the first to annotate the *A. lentiginosus* specimens at K. Gray did not indicate which of the sheets was the type nor did he annotate every sheet, but he was the first to recognize that the central element (K264945) on one of the types was *A. lentiginosus*. However, he did not recognize that the other two elements on this sheet were type material for *A. diaphanus* Douglas ex Hook. After Gray, the delimitation of typical *Astragalus lentiginosus* has largely been based on the morphology of specimens found in the vicinity of the Blue Mountains in Oregon. Since both *A. lentiginosus* var. *salinus* (Howell) Barneby and *A. lentiginosus* var. *platyphyllidius* (Rydb.) Peck can be found in southern Blue Mountains of Oregon, some populations of these taxa have been misinterpreted as typical *A. lentiginosus*. Barneby (1945) was the first since Gray to critically analyze the types of the *A. lentiginosus* complex and refine typical *A. lentiginosus* morphologically. The only Douglas specimen of *A. lentiginosus* he saw for this revision was the fragmentary type at GH. Barneby (1964, p.917) indicated a specimen a K found "near the source of the Wallahwallah and Utala rivers" was the holotype. This is the first step lectotypification of *Astragalus lentiginosus* (McNeill et al. 2006, Article 9.8). Unquestionably, Barneby selected a fruiting specimen at K as the lectotype of *A. lentiginosus* since he knew that Hooker (1831, p.151) indicated that "the flowers of this do not appear to have been seen by Mr. Douglas" and that "floribus - ?" was the only reference to flowers in the diagnosis. However, there are two sheets in fruit from the same individual at K: one from the Herbarium Benthamianum (K 264012) and one from Herbarium Hookerianum (K 264017). It is likely that Barneby chose the specimen from the Hooker Herbarium, however no specimens at K are annotated by him. The individual, K264017, is mounted with a specimen of *A. lentiginosus* var. *lentiginosus* collected by Dr. Lyall (K 264018). After an examination of the diagnosis and all the types of *A. lentiginosus*, the second step lectotypification was made herein to unambiguously specify which sheet, Kew accession number, and elements mounted on the sheet correspond to the lectotype in accordance with McNeill et al. (2006) Article 9.15. The second specimen, K 264012, is an isolectoype of *A. lentiginosus*.

Since the fruit of typical *Astragalus lentiginosus* is not by itself diagnostic, precise taxon delimitation based on the lectotype is not possible. Both fruit type and flower size are diagnostic features that distinguish typical *A. lentiginosus* from other sympatric varieties. *Astragalus lentiginosus* var. *salinus* has small whitish flowers (keel <9 mm) and thin walled, bladdery inflated pods. *Astragalus lentiginosus* var. *platyphyllidius* has

larger whitish flowers (keel 11–15 mm long) and thick walled, curved pods inflated only towards the base. Throughout its range, the fruit of *A. lentiginosus* var. *lentiginosus* can take both of these forms. The lectotype is a late season specimen with only mature, thick walled, curved pods inflated only at the base. The size of the flowers is unknown.

For a precise interpretation of nomenclaturally typical *Astragalus lentiginosus*, a flowering specimen was chosen from the original Douglas specimens. The epitype of *Astragalus lentiginosus* is designated herein (K264945; McNeill et al. 2006, Article 9.7) as the larger individual (keels 8–9 mm long) in the center of the sheet. It is mounted with two other fragmentary elements. Element 2 (K264015) is a fruiting specimen of *A. diaphanus*. Element three is mounted in two different places on the sheet, has received different accession numbers (K264016 and K264014), and is a flowering specimen of *A. diaphanus*. This entire sheet was from the Herbarium Hookerianum. Elements two and three are potential lectotypes or isolectotypes of *A. diaphanus* and will be discussed in a future publication (Alexander, in prep). The Douglas label is associated with a portion of element three and indicates it was collected "on the banks of streams on the southern branches of the Columbia." Presumably, the flowering *A. lentiginosus* element was collected at the same locality as the *A. diaphanus* elements. Alternatively, the epitype and the lectotype could have been collected from the same geographical vicinity since the Walla Walla and Umatilla Rivers are two of several southern branches of the Columbia River in northeastern Oregon.

Astragalus diphysus var. **albiflorus** A. Gray, Pl. Fendler. Novo-Mexicanae, Mem. Amer. Acad. Arts II. 4:34. 1849. *Astragalus lentiginosus* var. *albiflorus* (A. Gray) Schoener, Great Basin Naturalist 34:180. 1974. Protologue: "with the preceding [*Fendler 146* from "around Santa Fe," New Mexico]. No. 147." Type: U.S.A. Plantae Novo-Mexicanae [New Mexico]: [locality not specified on label], 1847, *A. Fendler 147* (holotype: GH 112365!; isotypes: GH 58715!, K 264023!, MO).

Notes.—When Barneby (1945) examined the Fendler types of *Astragalus diphysus* at GH, he only found one type specimen of *Astragalus diphysus* var. *albiflorus* A. Gray (*Fendler 147* GH58715). This sheet was part of a collection transferred from the herbarium of the Boston Society of Natural History to GH in 1941. Later, Barneby (1964, p. 940) noted that this specimen "was received long after Gray's death and not annotated by him," and selected an isotype at MO as the lectotype. Although not explicitly stated, Barneby may have chosen the MO sheet because GH58715 has an uncertain history and was mounted with an isotype of *Astragalus diphysus* var. *diphysus* (*Fendler 146* GH58716).

In this study, comparisons of GH types and duplicates distributed by Gray to other institutions revealed that Gray distributed specimens and preprinted labels with only a handwritten collector's number. After Gray published his manuscript, *Plantae Fendlerianae Novo-Mexicanae*, workers at the other institutions wrote determinations on their duplicates based his manuscript. The Fendler types examined for this study at GH have the determination written in Gray's hand on the original preprinted Plantae Novo-Mexicanae label. In 2002, a thorough search was conducted at GH of all the North American folders and types of *Astragalus*. The original holotype of *A. diphysus* var. *albiflorus* (*Fendler 147* GH112365) with the collection number and the determination written in Gray's hand was rediscovered. This type specimen was recently divided from another *Astragalus* collection and remounted on a new sheet, which is the likely reason that Barneby was not able to find the original type. Currently, GH112365 is mounted with an unaccessioned, non-type specimen of *A. lentiginosus* collected by Bigelow in 1883 in Albuquerque, New Mexico. The rediscovery of the holotype of *A. diphysus* var. *albiflorus* at GH nullifies Barneby's (1964) lectotypification (McNeill et al. 2006, Article 9.17a).

Astragalus lentiginosus var. **diphysus** (A. Gray) M.E. Jones, Proc. Calif. Acad. Sci. II 5:673. 1895. *Astragalus diphysus* A. Gray, Pl. Fendler. Novo-Mexicanae, Mem. Amer. Acad. Arts II. 4:34. 1849. *Tragacantha diphysa* (A. Gray) Kuntze, Revisio Gen. Pl. 2:944. 1891. *Cystium diphysum* (A. Gray) Rydb. Bull. Torrey Bot. Club 32:659. 1905. Protologue: "around Santa Fe [New Mexico]...No. 146." Type: U.S.A. Plantae Novo-Mexicanae [New Mexico]: [locality not specified on label], 1847, *A. Fendler 146* (holotype: GH 58714!; isotypes: BM, F, GH 58716!, K! [3 Sheets], MO, NY!, P).

Notes.—The valid name for what has been commonly known as *Astragalus lentiginosus* var. *diphysus* (A. Gray) M.E. Jones has been controversial due to conflicting interpretations of prior editions the International Code. Barneby (1964, p. 941) stated "strict adherence to the Rules of Nomenclature require that the earlier in the varietal rank [in his opinion *A. diphysus* var. *albiflorus*] takes precedence [over *A. diphysus* var. *diphysus*]." He rejected making a new combination, *A. lentiginosus* var. *albiflorus*, since it would result in "an absurdity and runs counter to common sense" of using the commonly recognized name. Based on her interpretation of the Article 11 of the 1972 edition of the International Code, Schoener (1974) concluded, "the name, var. *diphysus*, is anteceded by the name *A. diphysus* var. *albiflorus*...[and] the older name in the same rank has precedence" (p. 180). Schoener (1974) then made the new combination, *A. lentiginosus* var. *albiflorus* (A. Gray) Schoener. Some revisions (Welsh 1978; Isely 1998) have recognized Schoener's combination, while the most recent (Welsh 2007) has used Jones'. The most recent International Code (McNeill et al. 2006, Article 11.6 and 26.3) resolves this controversy. Two taxa were described by Gray (1849): first, *A. diphysus* (based on *Fendler 146*); and

second, *A. diphysus* var. *albiflorus* (based on *Fendler 147*). The later taxon, *A. diphysus* var. *albiflorus*, automatically creates the priorable autonym, *A. diphysus* var. *diphysus*. When both are recognized as synonyms, the combination, *A. lentiginosus* var. *diphysus*, that M.E. Jones made in 1895 has priority over Schoener's 1974 combination, *A. lentiginosus* var. *albiflorus*.

Astragalus lentiginosus var. **bryantii** (Barneby) J.A. Alexander, comb. nov. *Astragalus bryantii* Barneby, Proc. Calif. Acad. Sci. 4, 25:156. 1944. Protologue: "ARIZONA: at the head of Phantom Canyon in the Grand Canyon of the Colorado River, Coconino Co., 15 Dec. 1939. Collected by Dr. H.C. Bryant..." Type: U.S.A. Arizona: [Coconino Co.]: head of Phantom Canyon, in Grand Canyon, 15 Dec 1939, *H.C. Bryant s.n.* (holotype: CAS 293940!; isotype: US 1769041, internet image!).

Notes.—*Astragalus lentiginosus* var. *bryantii* (Barneby) J.A. Alexander has been hypothesized to be related to either *A. lentiginosus* var. *palans* (M.E. Jones) M.E. Jones or *A. lentiginosus* var. *mokiacensis* (A. Gray) M.E. Jones in historical and modern treatments (Barneby 1944, Barneby 1964, Barneby 1989, Isely 1998, Welsh 2007). Welsh et al. (2003) and Welsh (2007) determined that specimens in Utah previously identified as *A. bryantii* Barneby are *A. lentiginosus* var. *palans*. All full list of these putative *A. bryantii* specimens has never been published, but presumably among them are the specimens cited by Barneby (1964) and Welsh (2007): *Gaines 828*, *Gaines 1005*, and *Gaines 1009*, all from NAU. Although these specific specimens were not examined, Alexander (2008) did not find any specimen from Utah previously determined as *A. bryantii* Barneby or *A. lentiginosus* var. *palans* that has the unique pod morphology found in the populations in the Phantom Ranch vicinity of the Grand Canyon. As delimited by Alexander (2008), *A. lentiginosus* var. *bryantii* is confined to the canyon populations along tributaries of the Colorado River upstream and downstream of Phantom Ranch, Coconino Co., Arizona. As far as known, these populations are long-distance disjuncts from that of the nearest population of *A. lentiginosus* var. *palans*. In addition, the carpological variation found in the specimens of *A. lentiginosus* var. *bryantii* is distinct from that of *A. lentiginosus* var. *palans*. However, some pod characters do overlap with the range of variation found in populations of *A. lentiginosus* var. *wilsonii* (Greene) Barneby and *A. lentiginosus* var. *ursinus* (A. Gray) Barneby. Barneby (1944) theorized that this taxon was closely related to *A. lentiginosus* var. *mokiacensis*, a relationship that has been discounted in all modern treatments (Barneby 1989, Isely 1998, Welsh et al. 2003, Welsh 2007). Further investigation of habitat in the canyons of the Colorado River eastward from the nearest populations of *A. lentiginosus* var. *mokiacensis* at Emory Falls (*Clover 6079*, CAS!) and Quartermaster Canyon (*Goodding 15-41*, RM!) may reveal populations of *A. lentiginosus* var. *bryantii* intermediate to *A. lentiginosus* var. *mokiacensis*.

Astragalus lentiginosus var. **iodanthus** (S. Watson) J.A. Alexander, comb. nov. *Astragalus iodanthus* S. Watson, Bot. King. 70. 1871. Protologue: "in the foothills of Western Nevada from the Virginia to the West Humboldt Mountains; 4500–6000 feet altitude... [S. Watson] 269." Type: U.S.A. Nevada: [Pershing Co.]: West Humboldt Mountains [Humboldt Range, NE of Lovelock], Jun 1868, *S. Watson 269* [in part] (lectotype, designated by Barneby 1964:962: US 46909!; isolectotypes: GH!, NY!, YU).

Astragalus iodanthus var. *diaphanoides* Barneby, Leafl. W. Bot. 4:50. 1944. Type: U.S.A. Nevada: Washoe Co.: between Reno and Dewey, 10 Jun 1943, *H.D. Ripley & R.C. Barneby 5659* (holotype: CAS; isotype: RSA).

Astragalus iodanthus var. *vipereus* Barneby, Mem. New York Bot. Gard. 13:963. 1964. Type: U.S.A. Idaho: Owyhee Co.: on cobblestone bluffs near Bruneau, 31 May 1945, *H.D. Ripley & R.C. Barneby 6485* (holotype: CAS; isotypes: NY!, IDS, RSA).

Notes.—In his taxonomic revision, Alexander (2008) concluded that that there is not a high degree of morphological and molecular differentiation between *A. lentiginosus* var. *palans*, *A. iodanthus* and *A. pseudiodanthus* and continued separation of these taxa as separate species is not supported. The new combinations recommended in Alexander (2008) are made formal herein.

Traditionally, differences in pod morphology have been the basis for the separation of *Astragalus iodanthus* S. Watson and *A. pseudiodanthus* Barneby from *A. lentiginosus*. Both have a deciduous, mostly uniloculate to partially biloculate pod with a septum less than half the width of the locule. This feature does differentiate these two taxa from the varieties of *A. lentiginosus* with bladdery inflated, completely biloculate pods. The contrast appears so great that in other sections of *Astragalus*, these differences have been considered species-level indicators. When these two taxa are merged into the complex folds of *A. lentiginosus*, along with the widespread and morphologically diverse taxa allied with *A. lentiginosus* var. *palans* (some of which were also originally recognized as a species), they form a continuum of variation—morphologically and geographically. In the Mojave and Sonoran Deserts, *A. lentiginosus* var. *mokiacensis* and *A. lentiginosus* var. *maricopae* Barneby form the southern end of the continuum with persistent, mostly straight, tubular, scarcely inflated pods and a septum extending from one-half to slightly over three quarters the width of the locule. In the Colorado Plateau vicinity, *A. lentiginosus* var. *palans*, forms the central and eastern axis of the continuum with deciduous, mostly straight to nearly 180° curved, tubular to triquetrous, scarcely inflated pods and a septum from one-half to slightly over three quarters the width of the locule. In the Great Basin, *A. lentiginosus* var. *iodanthus* (S. Watson) J.A. Alexander and *A. lentiginosus* var. *pseudiodanthus* (Barneby) J.A. Alexander form the western axis of the continuum with deciduous, mostly 180° curved, triquetrous, scarcely inflated pods and a septum from one-quarter to less than one-half the width of the locule. Barneby (1964) was the

first to recognize this similarity. In his uniquely succinct style, he stated "this pair of species [*A. iodanthus* and *A. pseudiodanthus*] posses no character which cannot be matched somewhere in *A. lentiginosus*" (p. 911) and "it is often difficult or nearly impossible to separate flowering material of [*A. iodanthus*] from the polymorphic *A. lentiginosus*, from which it differs principally in a tendency to dorsiventral and triquetrous compression of the fruit, which is never inflated and commonly very strongly incurved... however in *A. lentiginosus* var. *palans*, the lace-ellipsoid, little inflated pod varies from erect to decurved and its section varies from round to triangular, so that sometimes the only technical differential character that remains is the broader septum" (p. 959–960).

Other varieties of *A. iodanthus* have been recognized in Barnbey (1964), Isely (1998) and Welsh (2007), but they are treated herein and in Alexander (2008) as synonyms. Results of population level morphological analyses in progress may warrant recognition of *A. iodanthus* var. *diaphanoides* Barneby and *A. iodanthus* var. *vipereus* Barneby at the varietal-level within *A. lentiginosus.*

Astragalus lentiginosus var. **micans** Barneby, Leafl. W. Bot. 8:22. 1956. PROTOLOGUE: "CALIFORNIA: lower slopes of sand dunes at southeast end of Eureka Valley, east of Inyo Mts., Inyo County, elevation 3050 ft. May 13, 1955 (fr.) *John C. Roos 6354*, and at the same place, elevation 3100 Ft., April 9, 1955 (fl.), *Munz & Roos 20851*. Cotypes... Rancho Santa Ana Bot. Gard." TYPE: U.S.A. CALIFORNIA: Inyo Co.: lower slopes of sand dunes at SE end of Eureka Valley, E of Inyo Mts., 13 May 1955, *J.C. Roos 6354* (LECTOTYPE, designated here: RSA 100179!; ISOLECTOTYPES: GH!, K!, NY! [2 sheets], OSC!, RSA 114694!, SD, UC! [2 sheets], US 2483071, internet image!); U.S.A. CALIFORNIA: Inyo Co.: on sand dunes at S end of Eureka Valley, E of Inyo Mts., 9 Apr 1955, *P. Munz & J.C. Roos 20581* (EPITYPE, designated here: RSA 100180!; ISOEPITYPES: NY!, OSC!, RSA 109974!, RSA 115975!, UC!).

Notes.—Barneby (1956) designated two syntypes (as cotypes) in the protologue: one with fruit (*John C. Roos 6354* RSA) and one with flowers (*Munz & Roos 20581* RSA). He did not state the herbarium accession numbers in this publication. In his monograph, Barneby (1964) kept the same format, as cotypes, and did not designate a lectotype. Welsh (2007) also kept Barneby's format but listed both as syntypes. The fruiting specimen, *Roos 6354* (RSA100179) is designated here as the lectotype (McNeill et al. 2006, Article 9.2 and 9.10). Although there are some mostly withered flowers on the lectotype and the isolectotypes, the best floral characteristics are found on the flowering syntype. To keep all of the material used in the original type description (and the original intention of the author) intact, the flowering specimen *Munz & Roos 20581* (RSA100180) is selected here as the epitype (McNeill et al. 2006, Article 9.7).

It should be noted that in his original type publication, Barneby (1956) mistakenly cited "*Munz & Roos 20851*" as the syntype at RSA. Also Welsh (2007) mistakenly stated that the RSA syntype was "*Munz & Roos 20815*". All syntype specimens at RSA bear the correct collection number, *Munz & Roos 20581.* Also all isosyntypes at various institutions listed above are labeled with the collection number, *Munz & Roos 20581.* There do not appear to be any types with labels bearing the typographical errors published by Barneby or Welsh.

Astragalus lentiginosus var. **oropedii** Barneby, Leafl. W. Bot. 4:135. 1945. PROTOLOGUE: "Kaibab Trail to Roaring Springs, Grand Canyon National Park, Coconino County, Arizona, 22 September 1938, fruct., *Eastwood & Howell No. 7064* (Herb. Calif. Acad. Sci. No. 262056). Also ibid., 23 June 1933, flor., *Eastwood & Howell No. 1054* (Herb. Calif. Acad. Sci. No. 211208, CO-TYPE)." TYPE: U.S.A. ARIZONA: Coconino Co.: Kaibab Trail to Roaring Springs, 22 Sep 1938, *A. Eastwood & J.T. Howell 7064* (LECTOTYPE, designated by Barneby 1989:158: CAS 262056!); U.S.A. ARIZONA: Coconino Co.: Kaibab Trail to Roaring Springs, 23 Jun 1933, *A. Eastwood & J.T. Howell 1054* (EPITYPE, designated here: CAS 211208!)

Notes.—Barneby (1945) designated two syntypes (as cotypes) in the protologue: one with fruit (*Eastwood & Howell 7064*, CAS) and one with flowers (*Eastwood & Howell 1054,* CAS). In his monograph, Barneby (1964) kept the same format and did not designate a lectotype. For the Intermountain Flora, Barneby (1989) listed *Eastwood & Howell 7064* as the holotype for *A. lentiginosus* var. *oropedii* Barneby, which effectively is a lectotypification (McNeill et al 2006, Article 9.8). The flowers of *A. lentiginosus* var. *oropedii* are the most diagnostic feature, so an epitype is needed for precise taxonomic application of this variety. The epitype of *A. lentiginosus* var. *oropedii* is designated herein as the flowering specimen designated by Barneby as a syntype, *Eastwood & Howell 1054* (CAS; McNeill et al. 2006, Article 9.7), a designation that leaves intact the material used in Barneby's original description.

Astragalus lentiginosus var. **pseudiodanthus** (Barneby) J.A. Alexander, comb. nov. *Astragalus pseudiodanthus* Barneby, Leafl. W. Bot. 3:99. 1942. *Astragalus iodanthus* var. *pseudiodanthus* (Barneby) Isely, Syst. Bot. 8:422. 1983. PROTOLOGUE: "NEVADA: in deep sands of the plateau north of Cactus Peak, about twenty miles southeast of Tonopah, Nye Co.: alt. 5500 ft, 3 Jun 1941, *Ripley & Barneby No. 3725.*" TYPE: U.S.A. NEVADA: Nye Co.: plateau N of Cactus Peak, about 20 mi SE of Tonopah, 3 Jun 1941, *H.D. Ripley, R.C. Barneby 3725* (HOLOTYPE: CAS 290405!; ISOTYPE: RSA, POM).

Notes.—For a more detailed discussion of the relationships between this taxon and *A. lentiginosus*, see the above treatment of *A. lentiginosus* var. *iodanthus*.

Barneby (1964) was the first to describe in detail of the degree of intergradation of *A. lentiginosus* var. *pseudiodanthus* and some populations of *A. lentiginosus* var. *iodanthus*. These intermediate populations are uncommon but spread throughout its range. It is likely that *A. lentiginosus* var. *pseudiodanthus* recently differentiated from several of these relictual, intermediate populations and became adapted to a stabilized sand dune habitat. Similar adaptations have occurred in populations of *A. lentiginosus* var. *variabilis* Barneby, *A. lentiginosus* var. *fremontii* (A. Gray ex Torr.) S. Watson and *A. lentiginosus* var. *stramineus* (Rydb.) Barneby (which may itself be a sand dune derivative of *A. lentiginosus* var. *fremontii* or *A. lentiginosus* var. *vitreus* Barneby).

Population level morphological analyses in progress, leading to an overall monograph of Section *Diphysi*, may provide more details on the taxonomic status of these sand dune variants.

ACKNOWLEDGMENTS

Numerous individuals provided advice, funding and encouragement during various stages of this project including: Wesley E. Niles; Aaron Liston; Richard Halse; Kathryn Birgy of the UNLV Herbarium; Arnold Tiehm and the Northern Nevada Native Plant Society (and the NNNPS Small Grants Program); Lisa Decesare of the Library of the Gray Herbarium, Harvard University; and the Moldenke Fund for Plant Systematics and the Hardman Fund at Oregon State University. Additional thanks go to the late R.C. Barneby and the Barneby Fund for Research in Legume Systematics, which funded a month of research at NY. The following herbaria's online databases were consulted for this project: CAS, DS, GH, JEPS, K, MO, NY, OSC, ORE, RSA, SD, UC, UCR, UCSB, UNLV, US, WILLU. I thank the curators and staff of the following herbaria for access to their collections or loans of their specimens: BRY, CAS, DS, GH, JEPS, K, NY, OSC, ORE, RENO, RM, RSA, UC, UNLV, US, WILLU. Arnold Tiehm and one anonymous reviewer provided useful reviews.

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THE TYPIFICATION OF *CROTALARIA ROTUNDIFOLIA* AND *CROTALARIA MARITIMA* (FABACEAE)

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ABSTRACT

Two species of *Crotalaria* (Fabaceae) native to the American Southeast have been confused in part because of the improper typification of *C. rotundifolia* Walter ex J.F. Gmel. and absence of a type for *C. maritima* Chapm.. A John Fraser specimen currently the neotype for *C. rotundifolia* is here demonstrated to be taxonomically different from the plant known to Thomas Walter, justifying the Fraser specimen be superceded by an appropriate neotype from South Carolina. A specimen from the type locality of *C. maritima* in southern Florida is here selected as neotype for that species.

RESUMEN

Dos especies de *Crotalaria* (Fabaceae) nativas al Sureste de América se han confundido en parte debido a la tipificación incorrecta de *C. rotundifolia* Walter ex J.F. Gmel. y a la ausencia de un tipo para la *C. maritima* Chapm. Un espécimen de John Fraser que es actualmente el neotipo para *C. rotundifolia* se demuestra aquí que es taxonómicamente diferente de la planta conocida por Thomas Walter, justificando que el espécimen de Fraser sea reemplazado por un neotipo apropiado de Carolina del Sur. Un espécimen del lugar tipo de *C. maritima* en el Sur de Florida se selecciona aquí como neotipo para esta especie.

Crotalaria (Fabaceae), section *Alatae*, is represented in the southeastern United States by six species (Windler 1974; Ward 2009). Two taxa in this complex—*C. rotundifolia* Walter ex J.F. Gmel. (1792), and *C. maritima* Chapm. (1878)—have been variously interpreted as one undivided species (Isely 1990; Wunderlin & Hansen 2003), one species of two varieties (Windler 1974; Duncan & Kartesz 1981), or two species (Small 1933; Senn 1939; Ward 2009). Though the variability and occasional intermediacy of individuals of these taxa is obvious, recognition of their populations as worthy of specific status has been hindered by the absence of type specimens that adequately represent their morphology.

The cornerstone of stability in the linkage between a plant and its scientific name is the existence of a single specimen to which each name is permanently fixed. This single specimen—the type—permits later investigators to know with exactness the form of the plant on which the original author based the new name. But an author does not always select a type, or the type may become lost through misfortune, or the type may in one way or another be found to be unrepresentative of the author's original concept. Wherever ambiguity is caused by a missing or defective type, it is helpful to future studies of the characteristics and classification of the plant that a type be determined or a defective type be corrected. The *International Code of Botanical Nomenclature* (McNeill et al. 2006) dictates the rules that govern such selection or correction.

Crotalaria rotundifolia is a familiar name but a poorly understood species. It has been mapped by Windler (1974, as his var. *vulgaris*) as extending from southeastern Virginia, south to central peninsular Florida, and west to southeastern Louisiana. *Crotalaria maritima* was mapped by Windler (1974, as his var. *rotundifolia*) as ranging from southeastern Georgia (one undocumented dot in South Carolina), to southernmost Florida, and sparingly west to southeastern Louisiana. Though these ranges greatly overlap and need adjustment where herbarium materials poorly represent the two entities, Windler's maps well demonstrate that on balance *C. rotundifolia* is northern, while *C. maritima* is significantly more southern.

The present task is to establish types that will assist in separation of the two taxa. No effort is made here to justify this separation; that analysis must await greater understanding of the gross morphology, chromosome counts, DNA morphotypes, and differences in habitat preferences. Though the more southern

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population, *Crotalaria maritima*, requires for its typification only selection of a neotype, the more northern population, *C. rotundifolia*, has a record of misinterpretation of its type that can be resolved only by a full review of its taxonomic and nomenclatural history.

REPLACEMENT NEOTYPE FOR *CROTALARIA ROTUNDIFOLIA*

Crotalaria rotundifolia, the more northern of the two taxa, was the second species (to *C. sagittalis* L., 1753) of this group to be recognized. The plant was first described by Thomas Walter (1788), using the name *Anonymous rotundifolia*, an impermissible combination (Ward 1962, 2007a; Wilbur 1962). [Walter's use of *Anonymos* has been proscribed (Art. 20.4).] Four years later J.F. Gmelin (1792) validated Walter's epithet, as *Crotalaria rotundifolia*. Gmelin was merely assigning Walter's plant to a familiar Linnaean genus, *Crotalaria*, and his specific description was a restructured and shortened version of the description provided by Walter. *Crotalaria rotundifolia* J.F. Gmel. was thus based on *Anonymos rotundifolia* Walter and whatever materials Walter may have seen and used. [To reflect this origin, authorship of the legitimate name is often cited "Walter ex Gmelin."]

Walter, a plantation owner in rural South Carolina, with no means of long-term dried-plant preservation and surrounded by an abundance of fresh materials, kept no specimens that can now be termed types (Ward 2007b). A folio herbarium at the Natural History Museum, London (BM), gathered by John Fraser, the Scottish plant explorer, contains a specimen of a small *Crotalaria*. The folio was photographed in 1946 by B. G. Schubert and the specimen was believed by M. L. Fernald to be Walter's "type" of *Anonymos rotundifolia* (Fernald & Schubert 1948). Later authors (Ward 1962; Wilbur 1962; Windler 1974) accepted this judgment. Though Fernald used only the term "type," his usage suggests the more precise term "holotype." But since (as described below) Walter could not have based his description on this Fraser specimen, the type designation has been corrected to "neotype," as authorized by the *Code*, Art. 9.8 (Ward 2007a).

The origin and content of the Fraser folio (best termed the Fraser/Walter herbarium) has been studied in detail (Ward 2006). Fraser was in the American Southeast only briefly, with opportunity to collect only during 1787. He gathered plant materials with enthusiasm but with little proficiency; Andre Michaux, who met and briefly traveled with him, spoke disparagingly of Fraser's botanical skills (Ward 2007b). Even so, Fraser returned to England with a collection of 690 mostly small, sometimes fragmentary, specimens from South Carolina and Georgia. Fraser also carried with him Walter's manuscript of the pioneer *Flora Caroliniana* (1788), for publication in London.

Before Fraser returned to England, Walter had opportunity to see and perhaps study Fraser's specimens. Attached slips indicate the specimens had not been named when seen by him (though many bore three-digit numbers assigned by Fraser). Walter's handwriting is now present on 368 of the surviving slips, with 345 representing his identifications and the remainder being his various comments and observations (Ward 2007b). [Fraser's hand is borne by only 230 slips, many merely his assignment of a Walter epithet to a specimen identified by Walter only to genus.]

The specimen that has been believed to be Walter's "type" is now numbered 67-D (Ward 2006). Its photograph has been published (Fernald & Schubert 1948, plate 1107 - an image described as "quite horrible" by John Lewis). A similarly poor image is available on commercial microfiches of the entire herbarium, and a digital image of better quality has been made available by the Museum. [None of these images is sufficient to show pubescence, a critical feature.] The specimen was examined in the 1890s by Britten & Baker (1897), in August 1962 by John Lewis (BM) at the request of the present writer, again in the 1970s by Norman Robson (BM) at the request of Windler (1974: 189), and yet again in July 1984 by the present writer.

Specimen 67-D (BM) is small, but not unrepresentative either of the Fraser specimens or the species itself, consisting of a stem with six branches, perhaps 25 leaves, two crumpled flowers, and a single pod. Its leaves are broadly elliptic to ovate or obovate, apically rounded, the larger ones ±8 mm. long, ±5 mm. broad.

The label of specimen 67-D is unusually ample, with the plant attached near one end by its stem hav-

ing been slipped through parallel cuts in the paper (Fraser's common method of affixing labels). The label is sufficient in size to have received a series of notations extending from (probably) 1787 into the 1960s. Almost hidden by the stem is a partially obscured (and thus readable only as *??6*) three-digit number in Fraser's hand, believed to be his collection number. The label also reads: "*Lupinus affinis*" in Walter's well-formed script; this is one of the 23 specimens in the Fraser collection whose label bears Walter's hand but was not identified by him. [Specimens 67-A, 67-B, and 67-C, mounted across top of the same folio page, were labeled in Fraser's hand as *Lupinus pilosus* (2 spms.) and *L. perennis*.] Alongside the specimen and writings by Fraser and by Walter is a more extended notation: "*confer / Anonymos sagittalis p. 181 / = A. rotundifolia Walt. / = Rhynchosia*," in the hand of Asa Gray, who examined the Fraser folio in 1839. Below the Gray notation a further entry reads: "*Crotalaria maritima Chapm. / det. John Lewis 1962*." Still another reads: "*Anonymos rotundifolia Walt. / Fl. Carol.: 181 (1788) / SYNTYPE / of / Crotalaria rotundifolia J. F. Gmel. / in Linn., Syst. Nat., ed 13 2:1095 (1792)*" in an undetermined hand (below and thus subsequent to the 1962 notation of Lewis).

The source of specimen 67-D is unknown. Fraser, unlike Pehr Kalm in the American Northeast and Andre Michaux throughout eastern America, left no account of his travels. But from occasional remarks on labels and from specimens obtainable only in clearly defined locations, it is known Fraser reached (among other more northern and western stations) the Altamaha River in southeastern Georgia (Ward 2006), well within the distribution of the more southern taxon, *Crotalaria maritima*.

Pubescence of the stems and leaves has been long recognized to differ between northern populations typical of *Crotalaria rotundifolia* and more southern populations assignable to *C. maritima*. Lewis (pers. comm., Aug. 1962) directed his analysis primarily to this feature, making comparison with other collections of the two taxa as identified by Senn (1939) and from locations appropriate to the northern and southern populations, respectively. In his words: "The critical difference is that the general level of the top of the indumentum in [*C. rotundifolia*; Lewis used *C. angulata*] is equal in height (from the substratum) to the thickness of the stem, while in *C. maritima* even the few spreading hairs do not reach this height." He found the indumentum of the Fraser specimen to be very worn on the more-mature parts of the stem, but even here "the sparse remnant is wholly appressed." Further, he found the leaf shape "not inconsistent" with that of *C. maritima*. Lewis' conclusion was that Senn would have placed the Fraser specimen in *C. maritima* if he had seen it. The present writer, with opportunity in 1984 to study the Fraser specimen directly, fully agreed with Lewis' conclusions.

Windler (1971, 1974) addressed the judgment of Fernald & Schubert (1948), as well as information given him by Robson and his own examination of a better-quality photo from the British Museum, and his understanding of the approximate ranges of these two taxa. In consideration of the variable and intergrading morphologies of the two populations, he chose to recognize the taxa at varietal level. He was compelled to conclude the "Walter" type was of the more southern population, which obligated him to base *C. rotundifolia* var. *rotundifolia* on Fraser's specimen. He then took the next logical step, by selecting a specimen from the northern population to represent the non-typical variant. He proposed the new name *C. rotundifolia* var. *vulgaris* Windler, and typified it with a specimen from Hampton County, South Carolina.

Windler's acceptance of the Fraser specimen as typical of the southern population and a specimen from the northern population as representing the non-typical variant had the unfortunate consequence of putting in place as type of *C. rotundifolia* a specimen that Walter, the author of that name, would not have recognized. Indeed, Walter (though he died in 1789) has himself had opportunity to speak to this issue. He annotated specimen 67-D as "*Lupinus affinis*," or "allied to *Lupinus*," a comment similar to his many Latin-based remarks throughout the folio (Ward 2007b). This notation well indicates he did not recognize the species, though by later nomenclatural fiat he has now been claimed its author!

Windler's use of varietal status has suppressed the incongruity of a Walter name being applied to a population of which its author had no direct knowledge. Thus persons who interpret the complex as undivided will see no issue, and those who use only varieties will scarcely be alerted. But, in the belief the two populations merit specific rank (Ward 2009), the present writer has long been intrigued of a proper solution.

The *Code* (McNeill et al. 2006) permits any name to be retained by the process of "conservation" (Art. 14). Though there are several subtleties, the usual process would involve a petition to change the type by which a name was determined, thereby changing the name itself. This petition must be of a form acceptable for publication in a specific international journal (*Taxon*). The petition would then be reviewed by a special committee for the appropriate taxonomic group, then by a senior committee, then by a future botanical congress. Disapproval at any level would negate the proposal. Here, a proposal might ask that the type of *Crotalaria rotundifolia* Walter ex J.F. Gmel. be replaced by a specimen more appropriate than the one provided by John Fraser.

A less complex and uncertain pathway exists by which the issue may be resolved. The *Code*, Art. 9.16, states: "A neotype selected under Art. 9.15 [the article permitting selection of a neotype] may be superceded if it can be shown to differ taxonomically from the holotype or lectotype that it replaced." This power does not exist if a holotype or lectotype is involved, for in each of those categories a specimen seen and used by the author would have priority. But a neotype, a replacement selected at a later date by another person, can possibly be an inappropriate choice as a replacement for the missing holotype.

Rejection of the Fraser specimen as the type of *Crotalaria rotundifolia* quite exactly conforms to the requirements of Art. 9.16. All investigators who have examined specimen 67-D or its images, even though in part working independently and without full knowledge of the work of others, have agreed this specimen matches the more southern population. Even its author, Thomas Walter, by his annotation has left testimony of his endorsement. Though it is permissible for an author to consider the variability within the group too slight to permit naming, most authors have recognized the two populations at some taxonomic rank. And there is no dispute that the one taxon is common in the area known to Walter, and the other taxon to be essentially absent. It thus follows that the specimen previously treated as the neotype of *Crotalaria rotundifolia* is taxonomically different from the specimen that Walter must have once held and used as the basis for his new name.

Since the conditions for invoking Art. 9.16 are fully met, it also follows that the Fraser specimen treated as neotype of *Crotalaria rotundifolia* may be superceded by a more appropriate specimen.

Crotalaria rotundifolia J.F. Gmel., Syst. Nat. 2:1095. 1792. Type: U.S.A. South Carolina. Hampton Co.: ca. 3 mi NW of Yemassee on SC Hwy 68, sandhill, 23 Jul 1967, *D.R. & B.K. Windler 2769* (neotype, designated here: NCU). This selection supersedes the previous selection of *J. Fraser 67-D, 1787* (BM) as neotype, as authorized by the Code, Art. 9.16.

The selected specimen is also the holotype chosen by Windler (1974: 193) for *Crotalaria rotundifolia* var. *vulgaris*. Windler's judgment is accepted in his selection of a specimen appropriate for the northern population. Although typification does not apply outside of rank, the use here of the same specimen as the type of *C. rotundifolia* obviates all uncertainty as to application of the name without regard for the rank employed.

NEOTYPE FOR *CROTALARIA MARITIMA*

Crotalaria maritima, the more southern of the two species, is somewhat more variable than its northern analogue, in that the leaves of some plants may range from ovate to linear. This variability has troubled investigators (Windler 1974; Isely 1990), but has then been put aside as a poorly understood property of the southern population. Other workers have separated the more clear-cut linear-leaved plants as *C. linaria* Small (1933) or *C. maritima* var. *linaria* (Small) Senn (1939). Though there is unquestioned intergradation, this linear-leaved population is also separated edaphically along the South Florida coastal dunes, and merits specific rank (Ward 2009).

With *Crotalaria linaria* removed, the remaining plants of the southern population are appreciably more uniform. A rare, recently described endemic, *C. avonensis* Delaney & Wunderlin (1989), with succulent leaves and loosely appressed pubescence, from near the southern end of the Lake Wales Ridge in central peninsular Florida, appears to be a local derivative. An erect species with leaves glabrous above, *C. purshii* DC., is known to hybridize with the southern population (Windler 1974: 202). An erect, usually annual

FIG. 1. Neotype for *Crotalaria maritima* Chapm., Bot. Gaz. 3:4. 1878. From: open dry sandy swale behind low coastal shell ridge, Middle Cape ("Palm Cape" of Chapman 1878, 1883), Cape Sable, Everglades National Park, Monroe County, Florida. Bulls-eye scale = 3 cm diameter.

species, *C. sagittalis* L., may hybridize with the northern plants here called *C. rotundifolia* (Windler 1974: 202), but appears not to overlap in range with the southern population.

The earliest name for the southern population is *Crotalaria maritima* Chapm. (1878, 1883). Chapman described his plant with elements unique to the southern population: "Stem low, much branched, pubescent with short appressed hairs; leaves simple, small, oblong, sub-sessile, very thick and succulent; stipules minute and narrowly decurrent, or none; raceme 2-flowered; legume smooth; ... Stem 6 in. high. Leaves 1 in. long. Flowers not seen" (slightly rephrased in 1883). He gave the place of collection, perhaps well known to Florida travelers in the 19th century, though now far from obvious, as "Sandy beach at Palm Cape, South Florida." His notation of "Flowers not seen" suggests the plant was not overly familiar to him. Windler (1974) did not trace this station; he noted Chapman's type only as "not located."

Chapman's home was in Apalachicola, in the central Florida panhandle. At least once he is known to have visited another early botanist, Dr. John Blodgett of Key West (who died in 1853). He made this journey by taking a small boat along the western Florida coast, stopping and apparently collecting along the way. He may have done so more than once, at least for part of the distance, in that along with the new *Crotalaria* he reported many other plants newly discovered in South Florida (Chapman 1878). The careful account of Florida botanical exploration by R.P. Wunderlin, B.F. Hansen & J. Beckner (in Wunderlin & Hansen 2000) reported no documentation of these journeys.

Old late-19th century maps of Florida, however, do record "Palm Cape" as the middle point of Cape Sable, on the southwestern tip of peninsular Florida. The Palm Cape beach is an obvious stopping-point for shallow-draft vessels moving along the southern shore. This location is now within the Everglades National Park, Monroe County, though it is still quite as remote—and perhaps less visited—as in Chapman's day. In April 1964 the writer, accompanied by a graduate student and two rangers, was able to reach the Cape. *Crotalaria maritima* was immediately obvious, broadly spreading in a dry sandy depression behind the front beach. Specimens were collected, and one has been selected as typical of *C. maritima* Chapm..

Crotalaria maritima Chapm., Bot. Gaz. 3:4. 1878. (**Fig. 1**). Type: U.S.A. Florida. Monroe Co.: Middle Cape ("Palm Cape" of Chapman 1878), Cape Sable, Everglades National Park, open dry sandy swale behind low coastal shell ridge, 18 Apr 1964, *D.B. Ward 3939* (neotype (and topotype), designated here: FLAS).

With recognition of the types selected here, *Crotalaria rotundifolia* Walter ex J.F. Gmel. again becomes the round-leaved, non-succulent, spreading-pubescent plant of the Carolina coastal plain and northern Florida, and *Crotalaria maritima* Chapm. again is recognized as the ovate-leaved, succulent, appressed-pubescent plant of peninsular Florida. These points of nomenclatural stability will serve as clearly understood data-points for further work addressing the morphological subtleties of these and related taxa.

ACKNOWLEDGMENTS

My involvement with these little "rattleboxes" has extended intermittently over many years. I am grateful to Jacqueline Patman (Mrs. Malchie Broughton), University of South Florida, who briefly joined me in study of these plants, terminated too quickly by her movement westward; to Donald Windler, Towson State University, Maryland, for keeping me abreast of his more detailed studies and remaining a friend to the present day; to Derek Burch, Plantation, once my student and field companion and permanently my wise advisor; to John Lewis, British Museum of Natural History, for answering in such wonderful detail (most not reported here) my queries on the weary specimens of John Fraser; to Robert L. Wilbur, Duke University, for counsel on matters of nomenclature; to Christine M. Housel for the Spanish translation of the Abstract; to Kent Perkins, University of Florida, for the plate of *Crotalaria maritima*; and to Thomas G. Lammers and James L. Reveal for meticulous and insightful suggestions in review of my manuscript.

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BOOK REVIEW

Lawrence E. Stevens and Vicky J. Meretsky (eds). 2008. **Aridland Springs in North America: Ecology and Conservation.** (Arizona-Sonora Desert Museum Studies in Natural History). (ISBN 978-0816526451, hbk.). University of Arizona Press, 355 S. Euclid Ave., Suite 103, Tucson, Arizona 85719, U.S.A. (**Orders:** www.uapress.arizona.edu, orders@uapress.arizona.edu, 1-800-426-3797). $75.00, 432 pp., 6" × 9".

This volume grew out of two symposia, one at the Arizona-Sonora Desert Museum in 2000 and the other at the Ecological Society of America meetings in 2002. The book represents concerns and issues developed from the symposia and others that grew from the panel discussions that followed.

The book begins with a series of chapters that address the issues of springs ecosystems, underground hydrology, a springs classification system, and insights on paleontology and paleoecology of springs. This is followed by a series of case studies of springs ecosystems and vegetation covering springs in Arizona, Coahuila, Mexico, and palm oases in the lower deserts of the Southwest. Ecological processes operating at springs are also discussed, looking at springs on the southern Colorado Plateau, Zion and Grand Canyon National Parks, and at terrestrial productivity of springs in comparison with adjacent uplands. Human activity and springs biodiversity are next explored, focusing on springs in northern Sonora and in southern Arizona. Discussions on groundwater pumping and fire follow this section as they are the most immediate and important threats of springs ecosystem integrity. This is followed by legal options for springs conservation; springs often fall into a legal crack as they are considered neither groundwater nor surface water. The concluding essay in the volume explores the critical issues of a need for improved inventory, management assessment, basic and applied research, conservation, and restoration of springs as well as the challenge of engaging the public in improving the care and restoration of springs ecosystems.

This book will appeal to a wide audience including the interested public and researchers at all levels. Recommended for general library audiences and research level collections.

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LECTOTYPIFICATION OF *CARDAMINE FLEXUOSA* (BRASSICACEAE)

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In 1796, William Withering (1741–1799) described a new species of Brassicaceae from England as *Cardamine flexuosa* With. The primary set of Withering's collections is held at BM (Stafleu & Cowan 1976), but upon inspection we found no specimens at BM for any taxa of *Cardamine* L. bearing his name or hand. There are also none of his own *Cardamine* specimens or those collected by others that he may have studied in other herbaria also known to house his material: BR, K, LINN, LIV, UPS-Thunb (Stafleu & Cowan 1976). Loss of type material for *C. flexuosa* With. has been previously reported (Marhold 1995; Lihova et al. 2006); however, a lectotype for *C. flexuosa* With. remains undesignated. In the absence of the holotype we refer to illustrations cited in the protologue to lectotypify *Cardamine flexuosa*. Withering cited the following three illustrations which serve as syntypes in the absence of other original material: t. 277 (Curtis 1777); t. 735 (Oeder 1770); *C. hirsuta* (Walcott 1778).

Here we designate one of these illustrations as the lectotype for *Cardamine flexuosa* With.:

Cardamine flexuosa With., Arr. Brit. Pl. ed. 3:578. 1796. (**Fig. 1**). TYPE: "Rookery at Edgebaston" (LECTOTYPE, designated here: Curtis t. 277, 1777).

The lectotype (Fig. 1) is a historical illustration from Curtis' *Flora Londonensis* (1777). This work is a collection of loose or bound plates depending on the copy, and some copies have been hand colored. There are both colored and black and white examples of plate 277. The plate is accompanied by a brief but thorough Latin description and an English translation (Fig. 2). Plate 277 is labeled as the closely related species *C. hirsuta*, but clearly illustrates the siliques angled away from the inflorescence, flexing nodes, and a densely hairy stem more typical of *Cardamine flexuosa* With. This plate undoubtedly refers to the taxon in Withering's original description of the species. Basal leaflets in the illustration are not totally congruent with what we have observed in the field and on herbarium specimens for the taxon, but the description accompanying the plate reads: "Lobes of the radical leaves vary much in shape and are frequently much rounder than the figure represents." The only other caveat to our determination here is that a detailed illustration of the androecium in the bottom right corner of the plate (labeled #3) cannot refer to *C. flexuosa* because it illustrates only four stamens when *C. flexuosa* always has six. Information given in the description accompanying the plate sheds some light on this problem. The main morphological difference between *C. hirsuta* and *C. flexuosa* is stamen number, *C. hirsuta* having four and *C. flexuosa* six. Curtis' illustration shows four stamens and gives the following information in the description: "The same plant, early in the spring, when the weather is cold, has only four stamina; as the summer advances, it has constantly six." We believe that Curtis was encounter-

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Fig. 1. Digital image of the lectotype for *Cardamine flexuosa* in W. Curtis' Flora Londinensis or, Plates and descriptions of such plants as grow wild in the environs of London. t. 277. [Courtesy of Missouri Botanical Garden Library.]

Cardamine Hirsuta. Hairy Ladies-Smock.

CARDAMINE *Lin. Gen. Pl.* Tetradynamia Siliquosa.

Siliqua elaſtice diſſiliens valvulis revolutis. *Stigma* integrum. *Cal.* ſubhians.

Raii Syn. Gen. 21. Herbæ tetrapetalæ Siliquosæ et Siliculosæ.

CARDAMINE foliis pinnatis, floribus tetrandris. *Lin. Syſt. Vegetab. p.* 497. *Sp. Pl. p.* 915. *Fl. Suec. n.* 587.

CARDAMINE foliis pinnatis hirſutis, pinnis ſubrotundis, ſtaminibus quaternis. *Haller Hiſt.* 472.

CARDAMINE *hirſuta. Scopoli Fl. Carn. n.* 817. *t.* 38.

NASTURTIUM aquaticum minus. *Bauh. Pin.* 104.

CARDAMINE impatiens altera hirſutior. *Raii Syn. p.* 300. The leſſer Hairy, impatient Cuckow-Flower or Ladies-Smock.

CARDAMINE foliis pinnatis, foliolis radicalibus ſubrotundo-cordatis; caulinis ovatis dentatis petiolatis. *Hudſon. Fl. Ang. ed.* 2. *p.* 295. *Lightfoot Fl. Scot. p.* 348.

RADIX annua, fibroſa, fibris albidis.

CAULIS ſpithamæus, et ultra pro ratione loci, in foſſis humidis reperitur etiam ſeſquipedalis, ſolidus, erectus, flexuoſus, ſulcato-anguloſus, prope baſin purpureus, et ſæpius hirſutiſſimus, ſuperne fere glaber, ramoſus, ramoſiſſimus etiam occurrit.

FOLIA radicalia plurima, in orbem poſita, pinnata, foliolis petiolatis, rotundato angulatis, plerumque quinque lobatis, hirſutis, punctis prominulis ſcabriuſculis, lobis inæqualibus, nunc obtuſis, nunc acutis, caulina anguſtiora et magis profunde inciſa, lobis paucioribus.

FLORES parvi, albi, primo vere tantum. tetrandri.

CALYX: Perianthium tetraphyllum, foliolis ovato-oblongis, obtuſis, concavis, deciduis, pilis paucis albidis inſtructis, *fig.* 1.

COROLLA: Petala quatuor, alba, calyce duplo fere longiora, patentia, integerrima, obtuſa, *fig.* 2.

STAMINA: Filamenta plerumque ſex, quorum duo, breviora, alba. Antheræ minimæ, luteſcentes, *fig.* 3.

PISTILLUM: Germen oblongum, tenue, ſtaminibus paulo brevior. Stigma capitatum, *fig.* 4.

PERICARPIUM: *Siliqua* erecta, uncialis, ſubcompreſſa, bivalvis, elaſtice diſſiliens, valvulis revolutis, *fig.* 5.

SEMINA duodecim circiter, ſuborbiculata, compreſſa, glabra, e flavo fuſca, *fig.* 6.

ROOT annual and fibrous, the fibres whitiſh.

STALK about a ſpan high, or more, according to the ſituation in which it grows; in wet ditches it is ſometimes found even a foot and a half in height, ſolid, upright, crooked, grooved or angular, purple near the baſe, and moſt commonly very hairy, above nearly ſmooth, branched, ſometimes very much ſo.

LEAVES next the root numerous, forming a circle, pinnated, the ſmall leaves ſtanding on footſtalks, round yet angular, generally divided into five lobes, hirſute, roughiſh with little prominent points, the lobes unequal, ſometimes blunt and ſometimes pointed; thoſe of the ſtalk narrower, and more deeply indented, with fewer lobes.

FLOWERS ſmall, and white, early in the ſpring having only four ſtamina.

CALYX: a Perianthium of four leaves, of an ovate, oblong ſhape, obtuſe, hollow, deciduous, furniſhed with a few white hairs, *fig.* 1.

COROLLA: four white Petals, almoſt twice the length of the calyx, ſpreading, entire and obtuſe, *fig.* 2.

STAMINA: for the moſt part ſix Filaments, of which two are ſhorter than the reſt, of a white colour. Antheræ very ſmall and yellowiſh, *fig.* 3.

PISTILLUM: Germen oblong, ſlender, a little ſhorter than the ſtamina. Stigma forming a ſmall head, *fig.* 4.

SEED-VESSEL: an upright *Pod*, about an inch in length, ſomewhat flattened, of two valves, which burſt with an elaſtic force, and roll back, *fig.* 5.

SEEDS about twelve in number, nearly round and flattened, ſmooth, and of a yellowiſh-brown colour, *fig.* 6.

We were inclined to believe with our ingenious friend Mr. Lightfoot, that the *Cardamine hirſuta* and *parviflora* were diſtinct ſpecies; but repeated obſervation and culture have convinced us, that they are both the ſame, varying only in ſize, in hairineſs, and in the number of their ſtamina.

In wet ſituations, where the ſoil is luxuriant, it grows a foot or two in height, and loſes in a great degree its hairineſs; in expoſed places it ſeldom reaches more than ſix or eight inches, and is generally much more hairy; and, when it grows ſingly, much more branched. The ſame plant, early in the ſpring, when the weather is cold, has only four ſtamina; as the ſummer advances, it has conſtantly ſix. The lobes of the radical leaves vary much in ſhape, and are frequently much rounder than the figure repreſents.

This ſpecies is by no means general about *London*, but abounds in particular places, as by *Chelſea* water-works, in wet ditches about *Hampſtead*, *Highgate*, and elſewhere.

It flowers in *April* and *May*. In the garden, if the ſituation in which it is ſown be ſhady, and the ſeaſon not uncommonly dry, it continues flowering and feeding during the whole of the ſummer.

According to Mr. Lightfoot, the young leaves are a good ingredient in a ſalad, and may eaſily be obtained in the ſpring, when Muſtard and Creſs are not to be had.

Fig. 2. Digital image of the description accompanying type illustration for *Cardamine flexuosa* in Curtis' Flora Londinensis or, Plates and descriptions of such plants as grow wild in the environs of London. Page previous to t. 277. [Courtesy of Missouri Botanical Garden Library.]

ing two different taxa during the course of the growing season. Our personal observations suggest that *C. hirsuta* has a winter annual life cycle and is only encountered in flower during the cooler months of spring. *Cardamine flexuosa*, on the other hand, does not have such a set life cycle in the landscape and can be seen flowering later in the year. We thus suggest that in the early Spring, Curtis was likely observing *C. hirsuta* with four stamens and later, when he observed six stamens, he almost certainly was observing *C. flexuosa* which is only subtly different in vegetative morphology compared with *C. hirsuta*.

The two remaining illustrations cited in the protologue (Walc. *C. hirsuta* and Fl. Dan.735) are poor representations of the taxon in question. The Walcott illustration labeled *C. hirsuta* (1778) depicts a plant with six stamens in the flower which could refer to *C. flexuosa;* however, a very straight stem and four stamens in the detailed drawing of the androecium suggest *C. hirsuta* rather than *C. flexuosa*. Table 735 (Oeder 1770) labeled *C. impatiens* exhibits a flexing stem, but the stem and rachis are very thick compared to *C. flexuosa* and there are numerous cauline leaves with leaflet shapes more typical of *C. impatiens*, though Kučera et al. (2006) excluded this as an accurate depiction of *C. impatiens* citing the lack of auriculate leaf bases. Compared to this illustration, *Cardamine flexuosa* has sparser cauline leaves which exhibit fewer leaflets per leaf than the basal leaves.

ACKNOWLEDGMENTS

We would like to thank the curators of BM, K, and LINN for the courtesies extended during herbarium visits, the curators at BR, LIV, and UPS-Thunb. for their assistance in searching for holotype material of this taxon, and those at MO for providing high resolution images of the designated lectotype. Reviews of Jeffery M. Saarela and Karol Marhold are greatly appreciated.

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AN INVESTIGATION OF MORPHOLOGICAL EVIDENCE SUPPORTS THE RESURRECTION OF *PYRROCOMA SCABERULA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Field data were gathered from 31 wild populations of *Pyrrocoma liatriformis* sensu lato (Asteraceae, Astereae). These are measures of degree of tomentosity and glandularity, number of lateral inflorescence branches, number, length and width of flower heads, width of phyllaries, and width of the lowest leaf of the inflorescence. Principle components analysis and univariate statistics of these characters reveal non-uniformity in the morphology of *P. liatriformis* sensu lato, with two identifiable morphologies corresponding to geographical range, as divided into the Palouse grasslands on the one hand and grasslands of the Snake River Canyons/Camas Prairie region on the other. The plants of the latter geographical range are represented by the type of *Pyrrocoma scaberula*, hitherto synonymized under *P. liatriformis* since the original publication of these names in 1909. The segregation of populations into a resurrected *P. scaberula* leaves *P. liatriformis* sensu stricto a much rarer and an even more threatened species. Conservation implications of this taxonomy are discussed.

RESUMEN

Se colectaron datos de 31 poblaciones salvajes de *Pyrrocoma liatriformis* sensu lato (Asteraceae, Astereae). Estos datos representan medidas del grado de tomentosidad, glandulosidad, número de ramas laterales de las inflorescencias, longitud y anchura de la cabezuela de flores, grosor de los filiarios, y anchura de la hoja inferior de la inflorescencia. Los análisis de componentes principales y los análisis univariantes revelaron falta de uniformidad en la morfología de *P. liatriformis* sensu lato, y también dos morfologías identificables correspondientes a la siguiente división geográfica: Los pastizales de Palouse y los pastizales del cañón Snake River / Pradera de Camas. Las plantas de la segunda región geográfica están representadas por el tipo *Pyrrocoma scaberula*, previamente bajo el sinónimo de *P. liatriformis* desde la publicación original de estos nombres en 1909. La segregación de esta población, con la resurgida *P. scaberula*, deja a la especie *P. liatriformis* sensu stricto más rara y aún más amenazada. Se discuten las implicaciones para la conservación de esta taxonomía.

Key Words: *Pyrrocoma*, Asteraceae, Astereae, Palouse, Snake River Canyon, Camas Prairie, principle components analysis

INTRODUCTION

Members of the genus *Pyrrocoma* Hooker (Asteraceae: Astereae) are taprooted, herbaceous perennials with basal rosettes and leafy stems topped by one to several flower heads with yellow ray florets. The genus is endemic to western North America, and includes 26 taxa as circumscribed in the most recent treatment (Bogler 2006). Between Hall's monograph of the genus in 1928 and Mayes' monograph in 1976, *Pyrrocoma* was generally merged along with numerous other genera under *Haplopappus*. Recent morphological and molecular work suggests that such a broad use of *Haplopappus* results in a polyphyletic assemblage (Clark et al. 1980; Morgan 1992).

Edward L. Greene presented the names *Pyrrocoma liatriformis* and *Pyrrocoma scaberula* in a single publication in 1909, and subsequently, the latter has been treated as a synonym of the former (Hall 1928, Mayes 1976, Hitchcock & Cronquist 1973). *Pyrrocoma scaberula* was represented in its type collection by poor material, and until the 1990's, further collections from populations in the region of the type locality were unknown. Upon the availability of these specimens, it became apparent that plants from the region of *P. scaberula* consistently share many of the morphological traits described for and apparent in the type of *P. scaberula*. These traits appear to make them morphologically and geographically separable from typical *P. liatriformis*.

Pyrrocoma liatriformis sensu lato is currently placed on the United States Fish and Wildlife Service's Species of Concern list. At the time of its first listing as a conservation priority, the species was thought to be found primarily in the Palouse grasslands, but in recent years, numerous large populations of the species in its broad sense have been located in the canyon grasslands in the vicinity of the Snake, Clearwater and Salmon Rivers (Mancuso 1997). These newly found populations all share morphological characteristics with the type of *P. scaberula*, which was also collected in this more southerly region (near the town of Forest, Nez Perce County, Idaho).

The present study aims to test 1) the morphological coherence of populations of *Pyrrocoma liatriformis* sensu lato, 2) whether any distinct morphologies correlate to geographical range, 3) whether all populations can be unambiguously assigned to either of the hypothesized morphological entities, and 4) whether a portion of the populations are comparable to the type of *P. scaberula* and so can be assigned that name.

METHODS

Plants of both of the hypothesized morphologies were studied in the field in 31 populations. Seventeen populations were sampled the Palouse grasslands in Whitman County, Washington, and Latah and northern Nez Perce Counties, Idaho. Fourteen populations were sampled in grasslands of the Snake River Canyon system and adjacent Camas Prairie in Asotin County, Washington, southern Nez Perce, Idaho and Lewis Counties, Idaho. These 31 populations constitute more than one third of the 91 known extant occurrences (K. Gray, pers. com., Kemper 2005) from throughout most of the known range of *Pyrrocoma liatriformis* sensu lato. In total, 322 plants were studied in the field, 201 of them from the Palouse grasslands, and 124 from the canyon/Camas Prairie grasslands.

Two additional populations were studied based on herbarium specimens only. Both of these populations were newly discovered in 2005 by other collectors and were not seen by the authors until after the conclusion of field work for the present study. These specimens were included in the study because they represent populations in areas where *Pyrrocoma liatriformis* was previously not known to grow (one specimen from Wallowa County, Oregon, and two specimens from Washington County, Idaho, both located far south of the Palouse grasslands).

Plants in the field surveys were chosen randomly on intervals along walkabouts following contours of the topology so as to sample plants on any occupied slopes, aspects and soil/moisture conditions. Eight variable morphological characters were assessed based on the hypothesis that they are informative of genetic lineage and hence taxonomic placement. Two of these characters are qualitative: 1) pubescence (tomentose, non-tomentose or intermediate), 2) glandularity (strongly, weakly or intermediate). Six characters used are quantitative: 3) number of lateral inflorescence branches longer than 1 cm, 4) number of flower heads, 5) length of flower heads (from the base of the lowest closely ensheathing phyllaries up to the tips of the highest-positioned phyllaries; three heads, the lowest highest and a middle one were measured), 6) width of flower heads (non-pressed; same heads measured for length), 7) width of the phyllaries (measured among the second or third ranks of phyllaries on the same heads as measured for head length and width), and 8) width of the lowest leaf of the inflorescence. All quantitative characters appear not to be interdependent, with no correlation between them having an r^2 value higher than 0.463 (head width with phyllary width).

From large populations, voucher specimens (one fertile stem each) were gathered for every sampled plant. Plants from small populations were vouchered nondestructively by use of digital photographs, taken with a ruler for scale. Photos will be archived in both digital and printed format at the Stillinger Herbarium, University of Idaho, where voucher specimens will be deposited as well.

Quantitative morphological characters were entered as continuous variables in principle components analysis (PCA) run on PCORD (MjM Software Design). Characters 3 and 4 were discarded from the PCA owing to the large number of aborted branches and heads, which was perhaps due to the severe drought that occurred throughout the study area in the year of the field season. Correlations of characters with the first and second axes were sought to determine which characters contribute most to any clustering pat-

terns. Points in the PCA graphs were matched to their geographical range, pubescence type, and degree of glandularity to visually seek any correlations between the discrete and quantitative variables.

Means and standard errors of morphological characters and hypothesis tests were generated using JMP Version 3.2.6 for Windows (SAS Institute). Correlated discontinuities were sought using the ranges and means of both individual plant data and population means arrayed by geographical range, pubescence type and degree of glandularity.

High-resolution images were examined of the type specimens of *Pyrrocoma liatriformis, Pyrrocoma scaberula*, and *Pyrrocoma suksdorfii* E. Greene, which is the third name synonymized under *P. liatriformis* in all treatments since the publication of all three names by E. Greene. All three are housed at the U.S. National Herbarium, and may be viewed at the type specimen register at http://ravenel.si.edu/botany/types.

RESULTS

All eight morphological characters reveal non-uniformity within *Pyrrocoma liatriformis* sensu lato (Table 1). Within- and among-population variation is seen in all quantitative variables, but pubescence type and degree of glandularity were strongly uniform within populations.

The principle components analysis reveals clusters of populations, separated along axis one, which accounted for 81.88% of the variation. Axes two through four had broken-stick Eigenvalues higher than their actual Eigenvalues, and are thus not further considered. Correlation coefficients were greatest with axis one for phyllary width (-0.5147) and head length (-0.5046).

For pubescence type, all populations scored for the tomentose and intermediate types overlap in the right cluster in the PCA graph, along with two populations scored as non-tomentose (populations KS and GR, Fig. 1). All other non-tomentose populations appear in the left cluster. Similarly, populations scored as weakly and intermediately glandular overlap within the right cluster, along with two of the populations scored for strong glandularity (populations KS and GR). The left cluster correlates to populations of the canyon/Camas Prairie grasslands, while all plants of the Palouse grasslands cluster on the right.

When plants are assigned to geographical range (Palouse grassland versus canyon/Camas Prairie grassland) without considering population means, the ranges of the quantitative variables are overlapping to varying degrees, but are all significantly different (Table 1). Population means assigned to geographical range reveals far less overlap in head length, head width, phyllary width, and leaf width, but no appreciable separation in lowest and highest values is seen in number of lateral branches and number of flower heads (Table 2). Two outlier low values for population means of the canyon/Camas Prairie plants occur for head length and phyllary width; when these outliers are disregarded, there is no overlap in the ranges for population means in phyllary width, and very little for head length.

Plants of the Palouse grasslands in all but two populations were strongly or intermediately tomentose, with the tomentum being lanate and distributed most densely on the phyllaries, but often throughout the entire plant. Plants of the canyon grasslands and two proximal populations on the Palouse (Kramer Prairie and Gross Road) often have harsh, curled hairs on the stems and inflorescence branches, but never on the phyllaries, and the hairs are never lanate. Degree of glandularity was distributed among populations almost perfectly concommitantly with the occurrence of tomentum, the exceptions being that some Palouse populations could be strongly tomentose but intermediately glandular, or intermediately tomentose and weakly glandular. All plants of the canyon/Camas Prairie grasslands were strongly glandular, with resinous-punctate glands being distributed most strongly on the phyllaries and usually also on the cauline leaves. Any glands among Palouse plants were limited to the phyllaries. Among the quantitative variables, the Palouse plants had a greater number of lateral inflorescence branches, more numerous flower heads, shorter and narrower heads, narrower phyllaries and narrower cauline leaves (Table 1).

The Kramer Prairie (KS) and Gross Road (GR) populations, though located on the Palouse grasslands, share the lack of tomentum and strong glandularity of the canyon/Camas Prairie plants. However, they are attributable to the Palouse-type morphology based on (means and standard errors, values for KS preceding

Table 1. Means, standard error, and ranges of quantitative morphological characters for plants assigned to geographical range. Asterisks following the characters indicate the significance of the ANOVAs comparing per-plant values by geographical range.

	Geographical range	
Character	Palouse	Canyon/Camas Prairie
Number of lateral branches*	2.39 ± 0.16(0–17)	1.78 ± 0.19(0–7)
Number of heads**	7.57 ± 0.34(1–57)	5.67 ± 0.39(1–33)
Head length (mm)***	11.79 ± 0.12(8–17(–18.5))	14.22 ± 0.14(9–)11–21)
Head width (mm)***	6.56 ± 0.10(4–10(–11))	8.71 ± 0.11(6–14)
Phyllary width (mm)***	1.90 ± 0.03(1–3(–3.5))	2.83 ± 0.04(1.5–)3–5)
Leaf width (mm)***	7.23 ± 0.21 (4–14)	10.45 ± 0.21(4–) 6–19)

Table 2. Ranges of population means of quantitative morphological characters for plants assigned to geographical range. Values in parentheses are single-observation outliers.

	Geographical range	
Character	Palouse	Canyon/Camas Prairie
Number of lateral branches	0.5–6.4	0.0–3.17
Number of heads	1.6–14.0	3.0–15.0
Head length (mm)	10.3–13.9	(8.5–)13.8–15.1
Head width (mm)	5.8–8.7	7.4–11.1
Phyllary width (mm)	1.4–2.3	(1.4–)2.3–3.3
Leaf width (mm)	5.0–9.4	9.3–15.4

in each case): head length (12.63 ± 0.35; 12.53 ± 0.35), head width (6.58 ± 0.23; 6.66 ± 0.18), phyllary width (2.29 ± 0.73; 2.27 ± 0.12), and leaf width (7.44 ± 0.57; 7.55 ± 0.59), though their mean number of lateral branches (0.53 ± 0.29; 1.36 ± 0.43), and number of flower heads (6.82 ± 0.78; 5.64 ± 0.71) fell near the means of the canyon/Camas Prairie plants.

The type specimen of *Pyrrocoma liatriformis* (C.V. Piper s.n. 29 August, 1903, Pullman, Washington, US) shows a tomentose plant lacking conspicuous glandularity. The number of lateral branches average 6.5 between the two stems, and the number of flower heads averages 9.0. Head length averages 12.03 mm (6 heads), phyllary width ranges 1.5–2.0 mm, and width of the lowest leaves of the inflorescence is 7.5 mm. The type of *Pyrrocoma scaberula* (A.A. Heller 3469, 29 July, 1896, Forest, Nez Perce County, Idaho, US) is a non-tomentose plant with conspicuous glands on the phyllaries. Each of the 4 non-damaged stems bears no lateral branches and a single flower head. The heads are 12.5 to 14.5 mm long, and the phyllaries are 2.2 mm wide or greater. The width of the cauline leaves is narrow (mean of 4.2) compared to other plants from the canyon/Camas Prairie examined in the present study. The type of *Pyrrocoma suksdorfii* is a tomentose plant with no conspicuous glandularity. The number of lateral branches average 2.0, and the number of heads per stem is 4.7. Head length ranges 10–11.5 mm, the phyllaries are under 2.0 mm long, and the cauline leaf width averages 6.0 mm.

DISCUSSION

Qualitative and quantitative characters reveal that *Pyrrocoma liatriformis* sensu lato is morphologically non-uniform, both within and among populations. Sorting plants and populations into geographical range between the Palouse grasslands on the one hand and the canyon/Camas Prairie grasslands on the other reveal that this variation is nonrandom and is correlated to geographical range. While geographical range does not account for all variation, there are clearly two arrays of morphology that are each coherent within their own geographical range. Further, narrow discontinuities in the arrays of morphological variation for half of the quantitative characters (Head length, Phyllary width and Leaf width) are concomitant when population

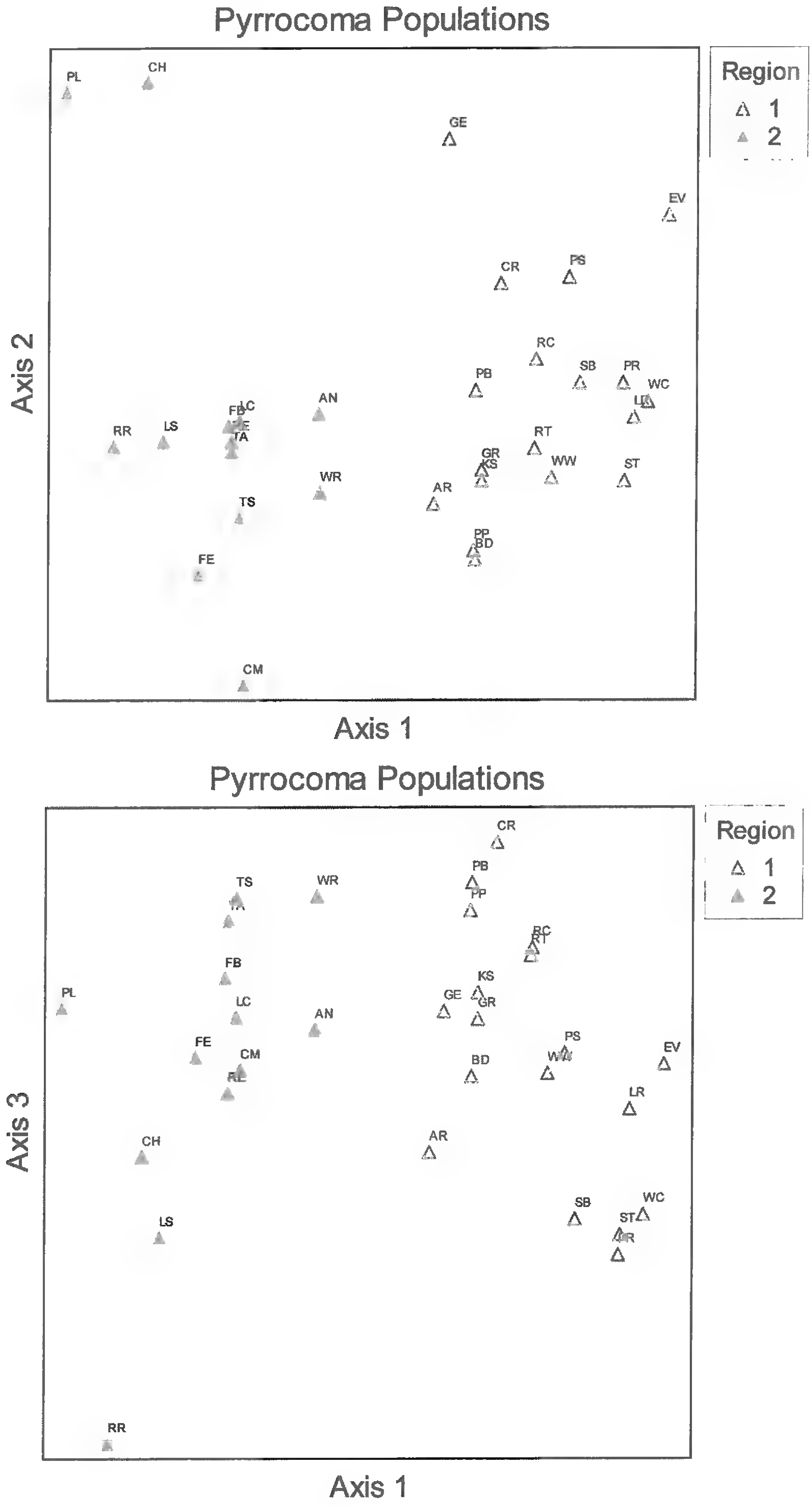

Fig. 1. PCA graph showing axes 1 versus 2, and 1 versus 3, respectively. The solid triangles represent populations of the canyon/Camas Prairie region. The open triangles represent the Palouse region.

means are sorted by geography. While there is considerable overlap in the remaining quantitative characters, and two of the Palouse populations break with their co-distributed populations in the qualitative characters, the distinctions among the most strongly diagnostic quantitative characters (Phyllary width, Head length, Head width and Leaf width) allows their placement within the Palouse morphology.

In the initial herbarium-based investigation comparing the Palouse and canyon/Camas Prairie morphologies within *Pyrrocoma liatriformis* sensu lato, a greater spread in means was found for number of lateral branches (3.86 ± 0.73 versus 1.54 ± 0.49, respectively) and number of flower heads (11.89 ± 1.86 versus 5.38 ± 1.07). Extreme drought occurred throughout the study area in the year of the field work, with very little precipitation falling in the preceding winter and spring, when normally the bulk of annual precipitation falls in both the Palouse and canyon/Camas Prairie regions. This suggests that under normal conditions, these two quantitative characters would be more diagnostic than is suggested by the data gathered from the field in 2005. Plants in all populations visited had a portion of their lateral branches and flower heads aborted, as evidenced by the number of small, distorted branches and heads that senesced without maturing flowers or fruits.

Examination of the type specimens of *Pyrrocoma liatriformis*, *Pyrrocoma scaberula*, and *Pyrrocoma suksdorfii* reveal that these plants are comparable to others collected from the same geographical regions in the present study. The observed morphologies of the Palouse grassland populations are clearly represented by the types of *Pyrrocoma liatriformis* and *Pyrrocoma suksdorfii*. The latter shows no appreciable distinction from the former, and its morphological characters fit within the ranges observed in the field for the Palouse populations in general, thus the name *P. suksdorfii* appears to be correctly synonymized under *P. liatriformis*. The type of *P. scaberula* fits well within the observed range of morphologies of the canyon/Camas Prairie populations (except in the width of the cauline leaves, which are within the range of the Palouse populations, and the anomalous single flower heads per stem, which was rarely observed in both geographical ranges). Thus, the type of *Pyrrocoma scaberula* appears to be representative of all populations of the canyon/Camas Prairie region.

KEY TO *PYRROCOMA LIATRIFORMIS* AND *PYRROCOMA SCABERULA*

1. Plants mostly heavily lanate-tomentose throughout, sometimes only on and near the flower heads; resinous-punctate glands usually absent or inconspicuous; population means of flower head length 10–13.8 mm; phyllaries 1.4–2.3 mm wide; population means for width of the lowest leaf of the inflorescence up to 9.3 mm; plants occurring in the Palouse grasslands ____ **Pyrrocoma liatriformis**
1. Plants hispid, any longer hairs harsh and firm, never lanate; resinous-punctate glands conspicuous, especially on the phyllaries; population means of flower head length 13.8–15.1, very rarely less; phyllaries 2.3–3.3 mm (very rarely less); population means for width of the lowest leaf of the inflorescence more than 9.3 mm; plants occurring south of the Palouse grasslands ____ **Pyrrocoma scaberula**

The degree of variation within *Pyrrocoma liatriformis* and *Pyrrocoma scaberula*, the overlap in certain characters, and the narrow discontinuities in both the geographical ranges and among the most diagnostic quantitative characters suggest a close relationship between the two. While the coherence of morphologies within the Palouse and canyon/Camas Prairie geographical ranges suggests that it is highly unlikely that the two species are randomly polyphyletic to each other, it is possible that one species is derived from the other (one monophyletic and the other paraphyletic), rather than both being derived from a now extinct common ancestral race (both monophyletic). Further, hybridization may have occurred giving rise to intermediate populations. The two Palouse populations here assigned to *Pyrrocoma liatriformis* which have the non-tomentose and strongly glandular condition of *Pyrrocoma scaberula* suggest either hybridization, or that these populations might actually be closer related to *P. scaberula*. It is also possible that specific taxonomic rank may be unmerited for *P. scaberula*, such that it would be best recombined as a variety of *P. liatriformis*. An ongoing molecular study will address these questions, assaying AFLP loci from all plants measured in the field in the present study.

Population means of head length, phyllary width and leaf width, along with the strong tendencies toward

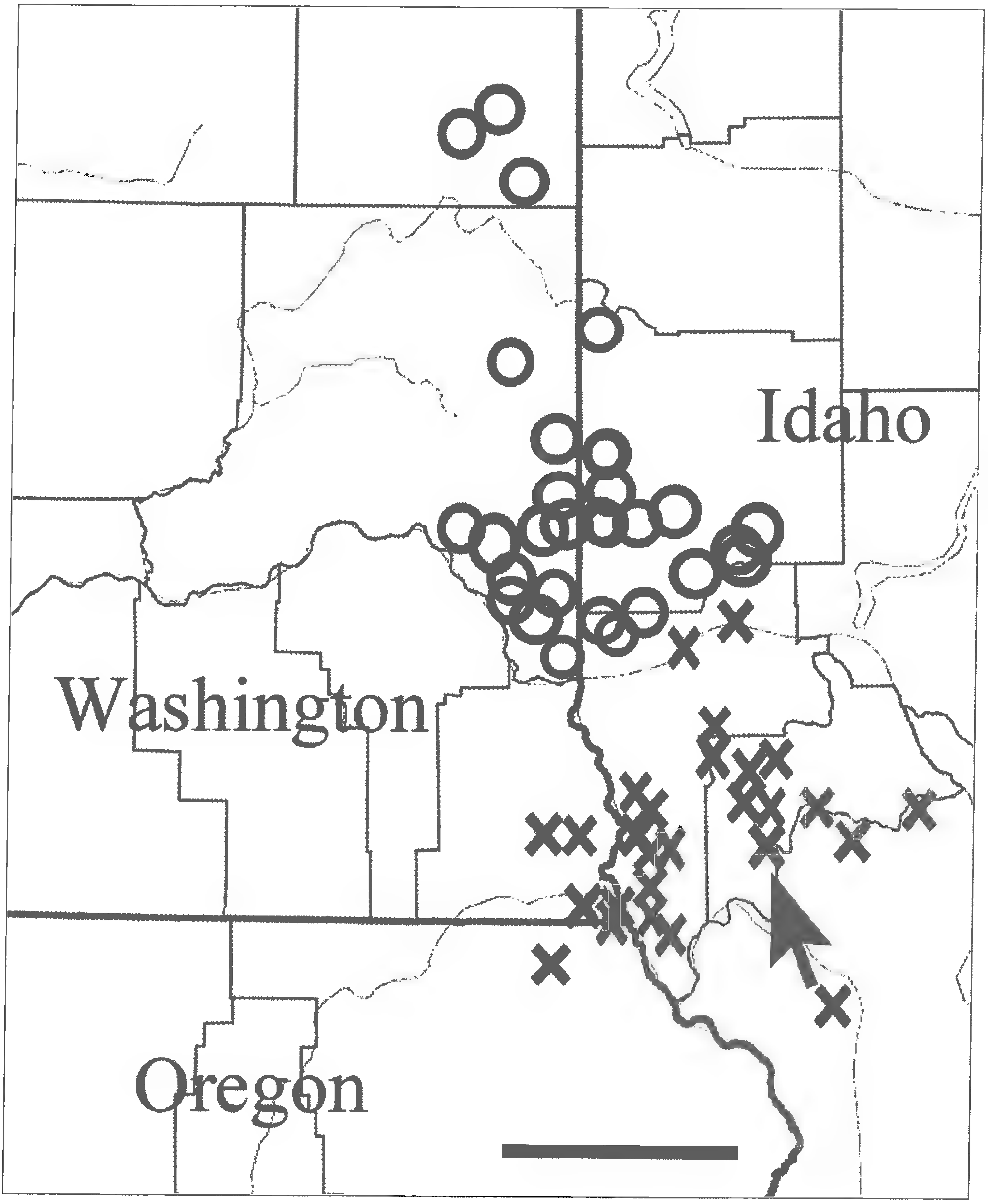

Fig. 2. Map showing locations of surveyed populations and additional herbarium specimens. Circles represent *Pyrrocoma liatriformis* and X's represent *Pyrrocoma scaberula*. The arrow points to the type locality of *Pyrrocoma scaberula*. The scale bar at the bottom represents 50 km. Not shown is the single known population in Washington County, Idaho, well to the south of the map range.

character states in the other morphological variables allow the unambiguous assignment of populations to either *Pyrrocoma liatriformis* or *P. scaberula*. Thus, the segregation of the relatively common and widespread *P. scaberula* leaves *P. liatriformis* sensu stricto as a very rare and highly threatened species. Several populations of *P. scaberula* are over 1,000 individuals (K. Gray, pers. comm.) and occupy large tracts of natural grassland, and the newly discovered populations in Wallowa County, Oregon and Washington County, Idaho suggest that additional populations may await discovery in the poorly explored grasslands of Hells Canyon in the intervening area. In contrast, nearly all of the populations of *P. liatriformis* are less than 500 individuals, and its potential habitats are all much smaller tracts surrounded by agricultural fields (Fig. 2). Intensive surveys in 2005 for additional populations in the Palouse grasslands by the present authors, as well as by the Idaho Conservation Data Center (K. Gray, pers. comm.) and Washington Natural Heritage Program (T. Kemper, pers. com.) in the same year make it highly unlikely that additional large populations will be discovered. Thus, *P. liatriformis* sensu stricto is vulnerable to extinction and should be protected accordingly.

ACKNOWLEDGEMENTS

This research was supported by funding from the U.S. Fish and Wildlife Service and Bureau of Land Management. We are very grateful for the enthusiastic assistance from the Idaho Conservation Data Center, the Stillinger Herbarium, University of Idaho, the Ownbey Herbarium, Washington State University, and especially to Karen Gray for the seed idea, and we thank Federico Osorio for the Spanish translation. David J. Bogler and an anonymous reviewer provided helpful comments.

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MISCELLANEOUS TYPIFICATIONS, ONE NEW SERIES, AND ONE NEW VARIETAL COMBINATION IN *CRATAEGUS* (ROSACEAE)

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ABSTRACT

Fifteen specific epithets and one varietal epithet in *Crataegus* (Rosaceae) are typified. These are: *C. brainerdii* Sarg., *C. subrotundifolia* Sarg., *C. brumalis* Ashe, *C. gravis* Ashe, *C. populnea* Ashe, *C. acutiloba* Sarg., *C. demissa* Sarg., *C. macrosperma*, *C. matura* Sarg., *C. pastorum* Sarg., *C. pentandra* Sarg., *C. roanensis* Ashe, *C. laurentiana* Sarg., *C. fernaldii* Sarg., *C. brunetiana* Sarg., and *C. laurentiana* var. *dissimilifolia* (the last four putative interserial hybrids). A new combination, **Crataegus chrysocarpa** Ashe var. **subrotundifolia** and a new series of central Asian *Crataegus*, **Altaicae**, are also proposed.

Key Words: *Crataegus* (Rosaceae), typifications, *Crataegus chrysocarpa* Ashe var. *subrotundifolia* (Sarg.) J.B. Phipps, comb. et stat. nov., North American, *Crataegus* ser. *Altaicae* J.B. Phipps, ser. nov.

RESUMEN

Se tipifican quince epítetos específicos y uno varietal en *Crataegus* (Rosaceae). Estos son: *C. brainerdii* Sarg., *C. subrotundifolia* Sarg., *C. brumalis* Ashe, *C. gravis* Ashe, *C. populnea* Ashe, *C. acutiloba* Sarg., *C. demissa* Sarg., *C. macrosperma*, *C. matura* Sarg., *C. pastorum* Sarg., *C. pentandra* Sarg., *C. roanensis* Ashe, *C. laurentiana* Sarg., *C. fernaldii* Sarg., *C. brunetiana* Sarg., y *C. laurentiana* var. *dissimilifolia* (híbridos putativos interseriales). Se proponen también una nueva combinación, **Crataegus chrysocarpa** Ashe var. **subrotundifolia** y una nueva serie de *Crataegus*, **Altaicae**, de Asia central.

INTRODUCTION

Until recently, most of the names used in the forthcoming treatment of North American *Crataegus* for Flora of North America, vol. 9, were not or not precisely, typified. This is gradually being rectified by the author, in part with various colleagues, by the typification of hundreds of names, for the most part those that will appear in the flora. Several important names from classical authors of the late eighteenth up to the later nineteenth century have now been typified, including e.g., *C. viridis* L., *C. crus-galli* L., *C. coccinea* L., *C. intricata* Lange, *C. flava* Aiton, *C. pruinosa* (H.L. Wendl.) K. Koch, and *C. rivularis* Nutt. However, by far the majority of names recently typified come from the 'explosion period' of *Crataegus* taxonomy, a time when the type concept was beginning to take hold, so only a few of these names prove to have holotypes. Of the major authors of this period, C.D. Beadle either cited cotypes (usually matching flowering and fruiting specimens from the same tree) in the protologue or designated them on the sheets and his taxa are generally straightforward to lectotypify. Beadle's types are mainly at US and NY. Charles S. Sargent normally indicated syntypes, either explicitly in his protologues or by annotating relevant specimens as "type" or simply '*n. sp.*'. There is virtually always adequate surviving material for lectotypification at A or GH, and sometimes duplicates elsewhere, the difficulties instead lying in selecting an appropriate lectotype from the putative types when slight discrepancies from the protologues are found, or if, sometimes, there are mixed gatherings. Further, there may be complications as a consequence of the tree numbering system in which various collaborators used the same number for a particular tree even when collecting at different dates. Sargent's names also present a challenge by their sheer number (832) but several hundred have now been typified. W.W. Ashe is the major author of this period whose names present the most difficult problems as his indications in the protologue of type, collector and location, are often poor, ambiguous, or even lacking

so that only the existence of handwriting by Ashe or one of his collectors remains to document authenticity. The dispersal of authentic Ashe material during his active period was to a wide range of herbaria so it can be difficult to track down, while his private collection, often poorly labeled and seemingly incomplete, had to await curation at NCU until after his death by T.G. Harbison, this a labor of love never completed. Added to all this, his protologues tend to have the least detail of these three authors, sometimes omitting characters considered essential today. This is unfortunate for Ashe created many potentially earliest names and certainly many important species names bear his authorship, e.g., *C. chrysocarpa, C. dodgei* and *C. margaretta* (since typified), *C. macrosperma, C. roanensis, C. holmesiana* (still untypified). Consequently, Ashe names usually require neotypification, and not surprisingly, there is little enthusiasm for entering this minefield.

This paper concentrates on several Sargent and Ashe examples to provide valid names for clearing up some taxonomic problems in ser. *Tenuifoliae, Brainerdianae* and *Rotundifoliae* and some putative interserial hybrids probably between ser. *Rotundifoliae* and *Macracanthae*. The text is also the vehicle for introducing the segregate central Asian series *Altaicae*.

A—*Crataegus* series *Brainerdianae*

1. Crataegus brainerdii Sarg., Rhodora 3:27.1901. Type: U.S.A. Vermont. Addison Co.: SW Middlebury, "Garrett House," 22 Sep 1900, *E. Brainerd 6b* (lectotype, designated here: A 2536, duplicate at A).

Comment.—This sheet, like the other two syntypes, has both flowering and fruiting material. The lectotype shows beautifully the characteristic leaf shape and the quite abundant, ± ellipsoid fruit.

B—*Crataegus* series *Rotundifoliae*

1. Crataegus chrysocarpa Ashe var. **subrotundifolia** (Sarg.) J.B. Phipps, comb. et stat. nov. Basionym: *Crataegus subrotundifolia* Sarg., Bot. Gaz. 35:394. 1903. Type: U.S.A. Illinois. Lake Co.: shores of Lake Zurich on bluff bank, 13 May 1901, *E.J. Hill 31a* (lectotype, designated here: A).

Comment.—A fruiting syntype, same label data except 5 Sep 1901, shows better the quite rounded short-shoot leaves on which Sargent based this species. However, as I am emphasizing the glabrous hypanthium and the not densely hairy inflorescence branches to particularize this, consequently widespread form, I prefer the flowering specimen for the type.

This variety is erected to accommodate those variants of *Crataegus chrysocarpa* with glabrous hypanthia and variably hairy inflorescences.

C—*Crataegus* series *Silvicolae*

1. Crataegus brumalis Ashe, Ann. Carnegie Mus. 1:393.1902. Type: U.S.A. Pennsylvania. Allegheny Co.: Pittsburgh, 18th Ward, Stanton Ave., corner of Morningside Road, *J.A. Shafer 19a*, 20 May1902 (lectotype, designated here: PH 648488).

Comment.—A quite good duplicate (PH 686552) exists as does some fruiting material with the lectotype. The stamens on the lectotype are said to be purple.

This taxon, often made a variety of *C. iracunda* Beadle, has ± glabrous adaxial leaf surfaces at anthesis and much broader truncate leaf-bases. Moreover, it is out of range for *C. iracunda* so it is best assigned to ser. *Silvicolae* as a scarce presumptive interserial hybrid. Most records of it are probable misidentifications of a form of *C. macrosperma*.

2. Crataegus gravis Ashe, J. Elisha Mitchell Sci. Soc. 20:49. 1904. Type: U.S.A. Michigan. St. Clair Co.: Port Huron, *C.K. Dodge Type Tree 28*, 26 May1902 (lectotype, designated here: MICH). Epitype: U.S.A. Michigan: St. Clair Co.: Port Huron, *C.K. Dodge Type Tree 28*, 7 Oct 1902 (lectotype, designated here: MICH, duplicate at MICH).

Comment.—This tree was apparently quite frequently collected and Kruschke (1965) mentions specimens at MSC and MIN. Unfortunately, this flowering syntype, the only one located, is of indifferent quality, so I am also epitypifying with a superior fruiting specimen from the type tree.

This species was said to be 'common' by Ashe but it has not been seen in the vicinity of Port Huron, including the very well-collected Sarnia area across the river in Ontario, in recent years. It is somewhat like *Crataegus pruinosa* var. *parvula* in general appearance but has slightly hairy adaxial leaf surfaces, a proportionately broader and slightly larger leaf, a larger and narrower fruit type, and lacks the elevated calyx of *C. pruinosa*.

3. Crataegus populnea Ashe, Ann. Carnegie Mus. 1:395.1902. Type: U.S.A. PENNSYLVANIA. Berks Co.: 2.5 mi NW of Kutztown, beyond Umbrella Hill, *C.A. Gruber 31*, 15 May 1902 (LECTOTYPE, designated here: PH).
Comment.—Two excellent fruiting specimens at PH dated 20 Sep 1903, have otherwise identical label data.

The type material confirms exactly the traditional interpretation of this fairly common northeastern species, which is followed in FNA vol. 9. The large leaves, especially at anthesis, and squarish lobe-tips of many of the leaves are characteristic.

D—*Crataegus* series *Tenuifoliae*

Forms of *C. macrosperma* that have been made into varieties have been selected for typification.

1. Crataegus acutiloba Sarg., Rhodora 3:23. 1901. TYPE: U.S.A. MAINE. Hancock Co.: Mt Desert, 4 Sep 1899, *B. Jones s.n.* (LECTOTYPE, designated here: A).
Comment.—A beautiful fruiting specimen, annotated by Sargent 'n. sp.' is selected for the lectotype. It has the characteristic large, cuneate-based, somewhat elongate (5–8 mm) leaves and narrow fruit that perfectly fits the protologue. Sargent considered this the characteristic large-leaved type of the coast from Massasuchetts Bay to Nova Scotia but cited neither specimens nor any precise localities.

An A specimen annotated 'type' by Kruschke is not supported in Kruschke (1965).

2. Crataegus demissa Sarg., Rhodora 5:139. 1903. TYPE: U.S.A. VERMONT. Chippenden Co.: Charlotte, 26 May1902, *F.H. Horsford s.n.* (LECTOTYPE, designated here: A).
Comment.—The lectotype is described as a 'small shrub' and has all the short-shoot leaves truncate to ± cordate, exactly fitting the protologue. A fruiting syntype collected by Sargent from Charlotte, Vt., is a good match. However, all the syntypes from Lennox, Mass., have mostly wide-cuneate leaf-bases, with only a few ± truncate.

This is a very distinctive, apparently dwarf, form of *C. macrosperma* but there appears to be little material from anywhere else closely matching the type.

3. Crataegus macrosperma Ashe, J. Elisha Mitchell Sci. Soc. 16:73. 1900. TYPE: U.S.A. ALABAMA. DeKalb Co.: Desoto State Park, woodland, 25 Sep 2001, *R. Lance 2170* (NEOTYPE, designated here: UWO).
Comment.—The neotype comes from the southern part of Lookout Mountain, the type locality. It is selected for its suborbicular fruit and leaves matching the protologue, except for their apices (see below).

Crataegus macrosperma is the most important taxon dealt with in this paper. Ashe gives the distribution as northern Alabama, northwestern Georgia and the adjacent portions of Tennessee, being frequent on Lookout Mountain in the last state (type locality) and in the surrounding mountains. Lacking authentic material and working with an inadequate protologue, my interpretation is affected by attempting to create, if possible, an entity in the *Tenuifoliae* that satisfies the protologue sufficiently and also differs from *C. roanensis*, the other common regional member of this series, which Ashe held to be different. There is little meaningful differentiation in the protologues except for range, *C. macrosperma* having 'round' versus 'oblong' fruit, a more southwesterly, lower altitude distribution, leaf blades 'deltoid' (perhaps extension shoots, this not specified) or 'oval', a rather generic term of that period. *Crataegus macrosperma* is also said to have leaves 'obtuse' at the apex, but nothing like that has been seen in series *Tenuifoliae*, to which the protologue fully applies in other respects. Thus I am assuming that this is a defect in the description. There are two extreme leaf types in the general region of the type areas of *C. macrosperma*. and *C. roanensis*, southwestern Appalachia, that broadly correlate with the different fruit types so I am typifying *C. macrosperma* on a specimen lacking cuneate leaf bases but having orbicular fruit. This, or a similar entity, appears to be a widespread form extending to the north of the range of the species though whether it merits varietal separation from *C. roanensis* requires further work. Certainly, apparent intermediates with *C. roanensis* occur.

4. Crataegus matura Sarg., Rhodora 3:24. 1901. TYPE: U.S.A. VERMONT. Addison Co.: N of Bristol village, 19 Sep 1900, *E. Brainerd 10h* (LECTOTYPE, designated here: A).
Comment.—A fine fruiting syntype specimen is selected for the lectotype. It has very large leaves to 9 cm long, broad ovoid fruit and a broader angle at the leaf-base than *C. acutiloba*.

Crataegus matura and *C. acutiloba* appear to represent poles of variation of large-leaved northeastern *C. macrosperma*. An A specimen annotated 'type' by Kruschke is not supported in publication.

5. Crataegus pastorum Sarg., Rhodora 3:24. 1901. Type: U.S.A. Massachusetts. Worcester Co.: West Boylston, 6 Oct 1900, *J.G. Jack 11* (lectotype, designated here: A).

Comment.—I agree with Kruschke that *C. pastorum* is simply an ordinary form of *C. macrosperma*. Sargent gave the area of occurrence from the Champlain valley (Vermont) and Berkshire Co. (Mass.), to central and southern Massasuchetts but cited no specimens nor any precise localities. There are, however, plenty of specimens labeled 'n. sp.' by Sargent from the stated area.

6. Crataegus pentandra Sarg., Rhodora 3:25. 1901. Type: U.S.A. Vermont. Rutland Co.: West Rutland, 17 Sep 1899, *W.W. Eggleston 1135* (lectotype, designated here: A).

Comment.—A fruiting syntype specimen is selected for the lectotype. It has quite large leaves to 6 cm long, large subglobose fruit and is somewhat similar to *C. matura* and *C. acutiloba*.

7. Crataegus roanensis Ashe, Bull. North Carolina Exp. Sta. 175:114.1900. Type: U.S.A. NORTH CAROLINA. Henderson Co.: Bearwallow Mountain, Sep 1994, *R.Lance 205* (neotype, designated here: NCU).

Palmer in 1946 made this a variety of *Crataegus macrosperma* eventually differentiating it by the depth of lobing of the leaves while Kruschke raised it to the rank of species. This attention was given even though the species had no formal type. Ashe gives the distribution as Yancey and Mitchell counties, North Carolina, especially about the base of Roan Mountain (on the Tennessee border of Mitchell Co.), saying that it is not common below 4000 ft but between 4000 and 6000 ft it is one of the most common thorns. Although, presumably, Ashe held this to be different from *C. macrosperma*, there is little differentiation in the protologues, this taxon having 'oblong' versus 'round' fruit. I find two extreme leaf types in the general region of the type areas for *C. roanensis* and *C. macrosperma* that broadly correlate with the different fruit types so I am typifying *C. roanensis* on a specimen with cuneate leaf bases and oblong fruit. Forms of the *macrosperma* complex with narrow fruit are widespread, extending to Wisconsin, Ontario and New England and warrant further study. Interestingly, the quite numerous specimens from Yancey and Mitchell counties at NCU better match *C. macrosperma* than *C. roanensis* as interpreted here.

E—Putative interserial hybrids

Taxonomic discussion of the following may be found in Flora of North America, vol. 9, which it is anticipated will be published later this year.

1. Crataegus laurentiana Sarg., Rhodora 3:77. 1901. Type: CANADA. Quebec. La Prairie Co.: La Tortue (outskirts of Delson), 8 Oct 1899, *J.G. Jack 40* (lectotype, designated here: A).

Comment.—The type has eroded nutlets and in Jack 40 (flowering) the petioles are virtually eglandular. The latter is a particularly fine specimen from the type locality. Flowering syntypes have pink anthers. Further syntypes, also Jack collections, come from La Tortue and Caughnawaga (same county).

2. Crataegus laurentiana Sarg. var. **dissimilifolia** Kruschke ex J.B. Phipps. Type: U.S.A. Wisconsin. Ashland Co.: Madeline Island, 1.5 mi S of La Pointe, 11 Sep 1950, *E.P. Kruschke K-49-145* (lectotype, designated here: MILW, duplicate of lectotype: A).

Comment.—The flowering co-type, same label data except 3 Jun 1949, would make an excellent epitype. Anthers of the latter are 'white'.

Crataegus laurentiana Sarg. var. *dissimilifolia* Kruschke, Milwaukee Public Mus. Publ. Bot. 3:35. 1965

Although Kruschke's protologue has the word type associated with the second, fruiting specimen of a matching pair, it is clear both from the consistency of his usage as well as from the labeling of the specimens, that he understands the pair as co-types, the first being the flowering specimen of the same collection number. Kruschke's only exception to this system is found in a few cases where he only collected a type at one season.

3. Crataegus fernaldii Sarg., Rhodora 5:166. 1903. Type: U.S.A. Maine. Aroostook Co.: U.S.A.: Maine: Aroostook Co.: Fort Fairfield, river thicket, 27 Sep 1901, *M.L. Fernald Cr. 21* (lectotype, designated here: A).

The sharp and deep lobing of the leaves and relatively broad breadth: length ratio is reminiscent of *C. chryso-*

carpa but the near-glabrous and near-eglandular petioles are more like *C. macracantha*. Pink anthers in a syntype of the same number (presumed type tree) could well originate from *C. macracantha* but would be very unusual in *C. chrysocarpa* while the somewhat eroded nutlets of the lectotype suggest intermediacy between the species discussed. In sum, this seems to be a broader-leaved, somewhat less villous *C. laurentiana*.

4. **Crataegus brunetiana** Sarg., Rhodora 5:164. 1903. Type: CANADA. Quebec. Quebec Co.: Montmorency Falls, 30 May 1901, *J.G. Jack 129* (lectotype, designated here: A).

This is rather similar to *C. laurentiana* but the leaves are proportionately wider, even more sharply lobed in flower and less hairy (rather as in *C. fernaldii*), the petioles at anthesis more glandular, the inflorescence branches of a less silky villosity and the anthers cream. The flowering syntype, *Jack 129*, has pitted nutlets like *C. laurentiana* while those of another syntype, *Jack 120*, do not.

F—*Crataegus* series *Altaicae*

Crataegus series **Altaicae** J.B. Phipps, ser. nov. Type: *Crataegus altaica* Lange (*Crataegus wattiana* Hemsley & Lace).

Similes ad ser. *Sanguineae*, ser. emend., sed cum fructibus luteis vel fuscis, non rubris vel atris, inflorescentiis glabris, non pilosis vel subpilosis. Distributio: Asia centralis occidentalis in montanibus. Species 1 vel 2(–3).

Series *Altaicae* is a small (1–2 or 3) species series widespread in Central Asia to the west of the central Asian massif which ranges from Baluchistan (Pakistan) to the northern slopes of the Altai in south-central Siberia. It is named for a species widely known as *C. altaica* Lange, perhaps synonymous with *C. wattiana*. The new series is segregated from ser. *Sanguineae*, with which it shares important characters of pitted nutlets and falcate basal bracteoles. However, it has glabrous inflorescences, a very unusual yellowish to tan fruit color and occurs, uniquely for sect. *Sanguineae*, in a semi-xeric upland climatic zone. Differently from sect. *Sanguineae* as here emended, ser. *Altaicae* may also have an unusual but here not uncommon form in the species complex *C. wattiana/altaica* which has very deeply lobed leaves and veins to the sinuses.

ACKNOWLEDGMENTS

The curators and staff of HUH and PH are thanked for their valuable cooperation, particularly Melinda Peters at Harvard who imaged many syntypes for me. James L. Reveal and Kanchi Gandhi provided valuable review comments.

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Kruschke, E.P. 1965. Contributions to the taxonomy of *Crataegus*. Milwaukee Public Mus. Publ. Bot. 3:1–273.

BOOK REVIEW

Graham Charles. 2003. **Cacti and Succulents.** (ISBN: 978-1-1861268726, pbk.). The Crowood Press Inc., The Stable Block, Crowood Lane, Ramsbury, Marlborough, Wiltshire SN8 2HR, England. (**Orders:** www.crowoodpress.co.uk, by phone 01-672-520320). $35.00, 192 pp., 8 3/8" × 10 3/4".

The author's aim in writing this book is to give any potential reader an insight into what the hobby of growing cacti and succulents is really like today. He explains what makes the hobby so much fun and how satisfying it can be. He has found through experience that growing cacti and succulents provides one with a perfect opportunity to relax— after all, nothing happens quickly in a succulent collection.

The author describes the special features of the plants and what you need to know to get the best out of them. His book is an essential guide to cacti and other succulents, featuring 420 color photos and a wealth of information on the plants and their cultivation. Beautifully illustrated and highly accessible, this guide is both an instructive practical manual and a rich source of reference. More than 250 different species or genera and their natural habitats are profiled and illustrated. Topics include: the unique nature of succulents; their natural environment; history, classification, and nomenclature; watering, feeding, general care, and propagation; pests and diseases; and profiles of cacti and other succulents. It is very much a hands-on book for the potential and experienced grower. Many techniques are illustrated step-by-step.

Lavishly illustrated, this is an indispensable guide for growers and enthusiasts. Recommended for public libraries and research collections, it will be of use to the general public, students, and experts alike.

Graham Charles is a National Cactus and Succulent Society judge and lecturer. He has been a grower since the age of twelve and brings a wealth of knowledge and information to the topic.—*Gary L. Jennings, Librarian, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

WHAT IS *RANUNCULUS GELIDUS* (RANUNCULACEAE)?

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ABSTRACT

The name *Ranunculus gelidus* is commonly used in North American literature for a widespread arctic-montane buttercup, but some recent American references have called this species *R. karelinii*, while Asian references use the names *R. gelidus* and *R. karelinii* for an endemic species of central Asia, and use the name *R. grayi* for the plant of eastern Siberia and western North America. *Ranunculus gelidus* is the correct name for a narrow endemic in the Tian Shan and Jungar Shan of central Asia, and *R. karelinii* is illegitimate (a superfluous replacement for *R. gelidus*). Populations from eastern Siberia and North America, which differ from *R. gelidus* in their straight (not inflexed) achene beak, smaller petals, and less deeply divided leaves, are correctly known as *R. grayi*. The section in which this species is placed is correctly called *Ranunculus* sect. *Epirotes* (Prantl) Benson—"*Ranunculus* sect. *Auricomus* Spach," used in some recent publications, is not valid.

RESUMEN

El nombre *Ranunculus gelidus* se usa comúnmente en Norte América para un ranúnculo común en la zona ártico-montana, pero algunas referencias recientes americanas han llamado a esta especie *R. karelinii*, mientras que en las referencias asiáticas se usan los nombres *R. gelidus* y *R. karelinii* para una especie endémica de Asia central, y usan el nombre de *R. grayi* para la planta del este de Siberia y el oeste de Norte América. *Ranunculus gelidus* es el nombre correcto para un endemismo de Tian Shan y Jungar Shan en Asia central, y *R. karelinii* es ilegítimo (un reemplazo superfluo de *R. gelidus*). Las poblaciones del este de Siberia y Norte América, que difieren de *R. gelidus* por el pico del aquenio derecho (no inflexo), pétalos más pequeños, y hojas divididas menos profundamente, deben llamarse *R. grayi*. La sección en la que debe incluirse esta especie debe nombrarse como *Ranunculus* sect. *Epirotes* (Prantl) Benson—"*Ranunculus* sect. *Auricomus* Spach," usada en algunas publicaciones recientes, no es válida.

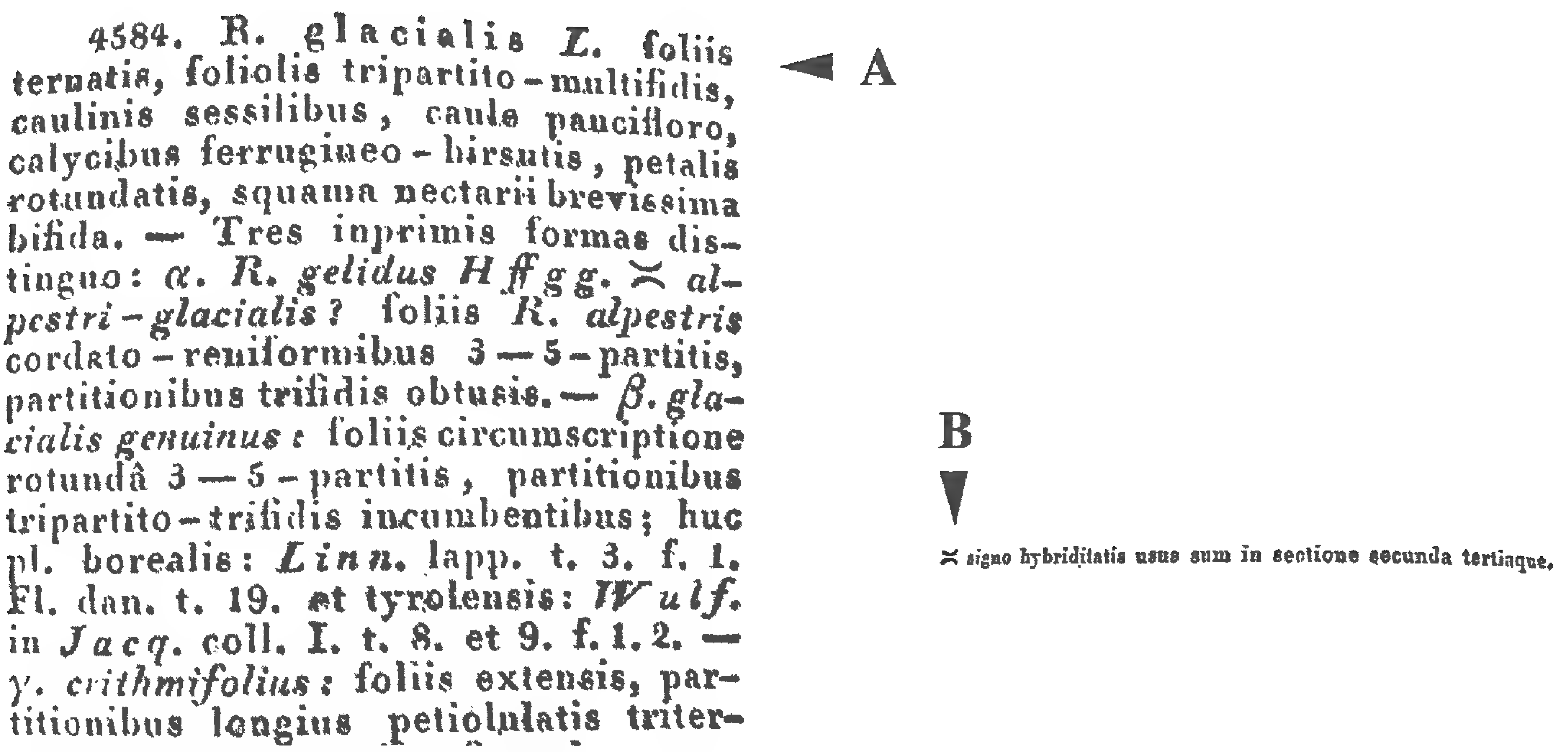
Treatments of *Ranunculus* in North America have generally used the name *R. gelidus* Karelin & Kirilov for a small buttercup that is widespread in arctic and alpine regions of western North America and eastern and central Asia (Benson 1948; Hitchcock & Cronquist 1964; Scoggan 1978; Whittemore 1997). However, a number of recent North American publications (Qian & Klinka 1998; Kartesz & Meacham 1999; Panjabi & Anderson 2006; Kratz 2007; NRCS 2008) treat this species under the name *R. karelinii* Czerep. This usage is questionable on several grounds. First, *R. karelinii* was not published until 1981, and three older names are listed in the synonymy of *R. gelidus* in North American references (*R. grayi* Britton 1891, *R. verecundus* B.L. Robinson ex Piper 1906, and *R. ramulosus* M.E. Jones 1912; Benson 1948; Hulten 1968a; Whittemore 1997). Second, recent Asian references (Ovchinnikov 1937; Baitenov et al. 1961; Voroshilov 1982; Tumokhina 1992; Cherepanov 1995; Borodina-Grabovskaya et al. 2001; Wang & Gilbert 2001) use the name *R. karelinii* for a species endemic to Central Asia, and treat specimens from eastern Siberia and North America as *R. grayi* Britton. Third, the name *R. karelinii* is superfluous and illegitimate according to IPNI (2008).

This widespread buttercup is currently going under three names (*R. gelidus*, *R. grayi*, and *R. karelinii*) in recent floristic literature, an unsatisfactory situation. The taxonomy and nomenclature of the species was investigated, as it relates to both the North American species and the type material from central Asia, to determine the correct name for the species.

NOMENCLATURE

Cherepanov (1981) concluded that *Ranunculus gelidus* Karelin & Kirilov 1842 is an invalid homonym because he felt that *R. gelidus* Hoffm. was validated earlier by Reichenbach (1830–33, p. 720). However, examination of this publication makes it clear that *R. gelidus* Hoffm. was not validly published. Reichenbach listed "R. *gelidus* Hffgg." under *R. glacialis* forma α, formatted like synonyms elsewhere in the book, not like names of other formae in the species (which have a single Latin epithet, not preceded by "R."; Fig. 1). Hoffmansegg's

J. Bot. Res. Inst. Texas 3(1): 245 – 250. 2009


4584. R. glacialis *L.* foliis ternatis, foliolis tripartito-multifidis, caulinis sessilibus, caule paucifloro, calycibus ferrugineo-hirsutis, petalis rotundatis, squama nectarii brevissima bifida. — Tres inprimis formas distinguo: *α. R. gelidus Hffgg.* ⨯ *alpestri-glacialis?* foliis *R. alpestris* cordato-reniformibus 3—5-partitis, partitionibus trifidis obtusis. — *β. glacialis genuinus:* foliis circumscriptione rotundâ 3—5-partitis, partitionibus tripartito-trifidis incumbentibus; huc pl. borealis: *Linn.* lapp. t. 3. f. 1. Fl. dan. t. 19. et tyrolensis: *Wulf.* in *Jacq.* coll. I. t. 8. et 9. f. 1. 2. — *γ. crithmifolius:* foliis extensis, partitionibus longius petiolulatis triter-

⨯ *signo hybriditatis usus sum in sectione secunda tertiaque.*

Fig. 1. A. Part of the description of *Ranunculus glacialis* from Reichenbach (1830–33 p. 720), showing the incidental mention of "*R. gelidus* Hffgg." associated with the description of *R. glacialis* forma α. B. A short excerpt from the "Praemonenda" of Reichenbach (1830–33 p. iv), explaining the unusual symbol in the discussion shown in part A.

unpublished name cannot be validated at the species level by its association with Reichenbach's description of a forma, so the supposed name "*Ranunculus gelidus* Hoffmansegg ex Reichenbach" does not exist. *Ranunculus gelidus* Karelin & Kirilov is therefore a valid name and is not a superfluous name as concluded by Cherepanov. The editors of IPNI are correct in concluding that it is *R. karelinii* Czerep., not *R. gelidus* Karelin & Kirilov, that is superfluous and illegitimate.

A second nomenclatural problem associated with these species is the correct name of the section to which the species belongs. North American publications (Benson 1948; Whittemore 1997) refer to it as *Ranunculus* sect. *Epirotes* (Prantl) Benson, while some recent European references (Tutin & Akeroyd 1993; Hörandl et al. 2005) refer to it as *Ranunculus* sect. *Auricomus* Spach. However, Spach (1839, p. 210) published this taxon at the rank of subgenus, not section, as already noted by Benson (1948). *Ranunculus* sect. *Epirotes* is thus the correct name for this taxon at the rank of section.

TAXONOMY

North American and east Asian material of this buttercup was considered conspecific with the central Asian *Ranunculus gelidus* by Ostenfeld (1909, p. 44). Benson, in his 1948 monograph of North American *Ranunculus*, explicitly stated that he had not seen central Asian material of *R. gelidus*, and was following Ostenfeld in treating North American material under this name. In order to evaluate the relationship of the North American buttercup to the type of *R. gelidus*, herbarium material from Central Asia (including isotype material of *R. gelidus*) was compared with North American material for characters used by Asian authors (Ovchinnikov 1937; Borodina-Grabovskaya et al. 2001; Wang & Gilbert 2001) to distinguish *R. gelidus s. str.* from similar species of *Ranunculus*. Several characters support the distinction of the Central Asian populations to which the type of *R. gelidus* belongs from the North American and east Asian plant.

First, Asian references emphasize trifoliolate leaves with petiolulate leaflets in *Ranunculus gelidus s. str.* North American and Siberian plants referred to *R. gelidus s. lat.* or *R. grayi* are described as having the leaf blade 3-parted but not compound (Benson 1948; Voroshilov 1982; Tumokhina 1992; Whittemore 1997). Leaf morphology is somewhat more variable than the literature suggests, and North American specimens rarely may have the blade of the basal leaves divided to the base and thus technically compound, but the leaflets are sessile, a condition not seen in specimens or in published descriptions of central Asian *R. gelidus*

s. str. The shape of the leaf segments also differs, with the ultimate segments being oblanceolate to obovate in Central Asian specimens and narrowly oblong or linear in North American specimens. Stem leaves often have narrower segments than basal leaves, but they also never have well-defined petiolules in North American material. The range of variation in the two regions is certainly different.

Second, North American and Siberian material that has been assigned to *Ranunculus gelidus* has the petals only 3–6 mm long, scarcely longer than the sepals. Isotype material of *R. gelidus* and other Central Asian specimens, however, have larger petals, 7–9 mm long (to 10 mm according to Wang & Gilbert 2001), about twice as long as the sepals.

Third, the achenes of North American and Siberian material that has been assigned to *Ranunculus gelidus* show a morphology similar to most members of *Ranunculus* sect. *Epirotes* (Prantl) Benson, with the beak of the fruit parallel to the long axis of the achene. In Central Asian specimens, however, the beak is displaced, originating on the adaxial side of the achene at an angle of ca 90° to the axis of the achene. This character is unusual in the genus, and was emphasized by Ovchinnikov (1937) in erecting *Ranunculus* cycle *Gelidi* Ovch. for two Central Asian species, *R. gelidus* and *R. rufosepalus* Franch. The unusual insertion of the achene beak was not mentioned in the Flora of China (Wang & Gilbert 2001), but is well developed on plants seen from the very narrow range of the species in China (*Yunatov et al. 948*, MO).

Other characters show considerable overlap, but still seem to show different ranges of variation in Central Asia and North America: thus, Central Asian plants always have solitary flowers, while North American material has 1–5 flowers per stem.

It seems clear, then, that Porsild (1943), Benson (1948), and Whittemore (1997) were wrong in treating the North American plant under the name *Ranunculus gelidus*, and recent authors who have used *R. karelinii* are incorrect on both taxonomic and nomenclatural grounds. The correct name for this buttercup is *R. grayi*, as used by Old World (and earlier North American) authors. It is unfortunate that it is necessary to introduce a third species name for these plants to the North American literature, but the name change is necessary to eliminate the incorrect application to North American plants of names belonging to a Central Asian endemic and reflect the true relationships of the North American plants. The following taxonomy ensues:

KEY TO *RANUNCULUS GELIDUS SENSU* FLORA OF NORTH AMERICA

1. Achene beak sharply inflexed so it is ± perpendicular to axis of achene. Petals 7–9 mm long, ca. twice as long as sepals. Central Asia _____ **Ranunculus gelidus**
1. Achene beak parallel to axis of achene. Petals 3–6 mm long, scarcely longer than sepals. North America, eastern Siberia _____ **Ranunculus grayi**

Ranunculus grayi Britton, Bull. Torrey Bot. Club 18:265. 1891. (**Fig. 2 E–H**). *Ranunculus pedatifidus* Hook., Fl. Bor.-Amer. 1:18, pl. 8 fig. B. 1829, not of Smith, The Cyclopaedia; or, Universial Dict. Arts,... 29: *Ranunculus* n. 72. 1818. *Ranunculus hookeri* Regel, Reis. Sud. Ostsib. Bot. Abt. 1:47. 1861, not of Schlechtendahl, Linnaea 5:210, 425. 1830. *Ranunculus drummondii* E. Greene, Erythea 2:192. 1894, nom. superfl. *R. gelidus* subsp. *grayi* (Britton) Hultén, Ark. Bot. (n.s.) 7:59. 1968. Type: "Barren summits of the Rocky Mountains, on the eastern side of the ridge, lat. 52° to 55°, *Drummond*."

Ranunculus verecundus B.L. Robinson ex Piper, Contr. U.S. Natl. Herb. 11:274–275. 1906. Type: WASHINGTON. Yakima Co.: Mount Paddo (=Mt. Adams), alt. 6000–7000 ft, *W.N. Suksdorf 93* (holotype: GH 38452)

Ranunculus ramulosus M.E. Jones, Contr. W. Bot. 14:47. 1912. Type: MONTANA: Border of Glacier and Flathead Cos.: Swift Current Pass, Glacier National Park, 11 Aug 1910, *M.E. Jones s.n.* (holotype: POM 100150)

Ranunculus gelidus var. *shumaginensis* Hultén nom. inval., Ark. Bot. (n.s.) 7:59. 1968, Madrono 19:223. 1968. Hultén's Arkiv for Botanik paper has only the name and a Latin diagnosis, with no mention of a type specimen at all. The Madrono reference merely adds, "Type in S," but gives no specimen information. Since there is no reference to a single specimen or gathering, the name is invalid (McNeill et al. 2006, art. 37.1–37.2).

Plants erect or decumbent from short caudexes, 3–22 cm. Roots slender, 0.5–1.0 mm thick. Leaves and stems glabrous or sparsely spreading-pubescent with long weak hairs, pedicels pubescent or glabrous. Basal leaves cordate or reniform, 0.5–1.8 × 0.8–3.0 cm, 3-parted (rarely 3-foliolate with sessile leaflets); segments again lobed, ultimate segments narrowly oblong or linear, 1.5–4 mm wide. Cauline leaves often larger, more deeply

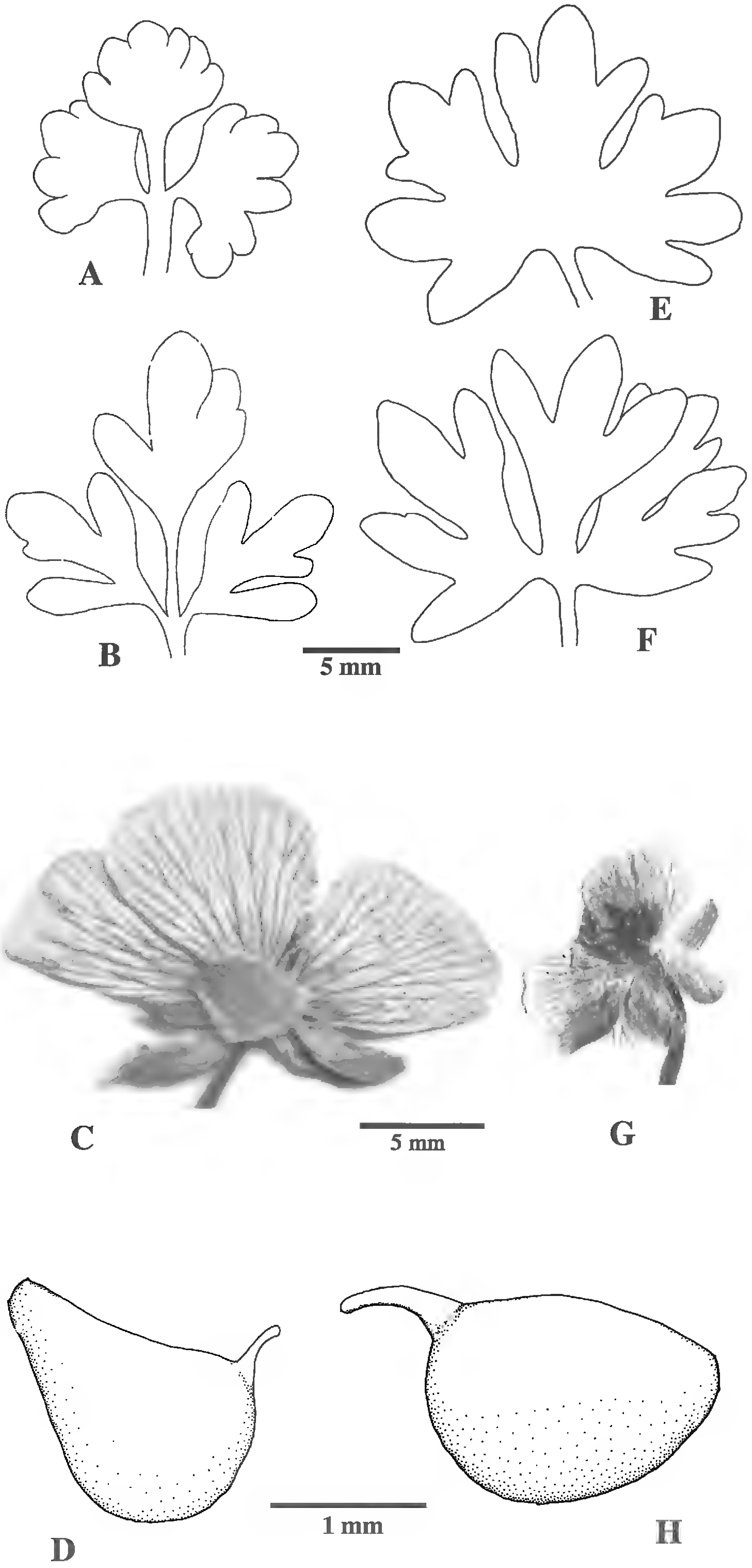


Fig. 2. Morphology of the two *Ranunculus* species. *Ranunculus gelidus*, A–B basal leaves, C a flower, D an achene. *Ranunculus grayi*, E–F basal leaves, G a flower, H an achene.

lobed, and with narrower segments. Flowers 1–5 per stem. Sepals 3–5 × 1–4 mm, pubescent or glabrous; petals 3–6 × 1–5 mm; receptacle glabrous or pubescent. Achenes 1.2–2.4 × 0.8–2.0 mm, glabrous, beak 0.4–0.8 mm, subulate, curved or hooked, parallel to axis of achene.

Seepy places in open rocky slopes and meadows, arctic and alpine. Widespread in western North America (from Alaska south to Oregon and Colorado; Benson 1948; Hitchcock & Cronquist 1964; Scoggan 1978; Whittemore 1997) and eastern Asiatic Russia (from the Lena Valley and the mountains east of Lake Baikal east to the Chukotka Peninsula; Voroshilov 1982; Tumokhina 1992; Cherepanov 1995).

Representative specimens examined: **CANADA. British Columbia:** clay run in rock crevice, Tenquille Lake area, Crown Mtn., 6000–6500 ft, *K. Beamish & F. Vrugtman 60938* (US); alpine slopes of Chipuin Mtn., Marble Mts., 6000 ft, *J.W. & E.M. Thompson 579* (US). Alpine slopes of Bluster Mtn., Marble Mts., 7000 ft, *J.W. & E.M. Thompson 384* (US). **U.S.A. ALASKA: Yakutat Co.:** head of Russell Fjord, *F.V. Coville & T.H. Kearney Jr. 940* (US). **Southeast Fairbanks (ca) Co.:** west-facing on small talus rhyolite, central N-S ridge of Sugarloaf Mtn., Healy (D-4), 63° 45 1/2' N, 148° 49' *W.S. Carwile 80-39* (US). **IDAHO. Blaine Co.:** alpine slopes at head of Boulder Creek Canyon, Sawtooth Mts., 10,000 ft, *J.W. Thompson 14100* (US). **Custer Co.:** Slide rock, 8000 ft, Bonanza, *J.F. Macbride & E.B. Payson 3394* (US). **MONTANA. Glacier Co.:** moist rocky slopes, frequent; vicinity of Sexton Glacier, 1950–2200 m, Glacier National Park, *P.C. Standley 17230* (US). **Judith Basin Co.:** Long Baldy, Little Belt Mts., 7000 ft, *J.H. Flodman 469* (US). **OREGON. Harney Co.:** alpine mountain meadow, Dino Creek headquarters, Steen's Mtn., 9000 ft, *P. Train s.n. 31vii35* (NA). **WASHINGTON. Pierce Co.:** rocky ridges and ledges, inter glacier, Mt. Tahoma (=Mt. Ranier), 7500 ft, *J.B. Flett 2177* (US). **Yakima Co.:** alpine slopes of Mt. Aix, 7500 ft, *J.W. Thompson 15046* (NA, US); on volcanic sand and gravel, Mount Paddo (=Mt. Adams), ca. 2400 m, *W.N. Suksdorf 4142* (US).

Ranunculus gelidus Karelin & Kirilov, Bull. Soc. Imp. Naturalistes Moscou 15:133. 1842. (**Fig. 2 A–D**).

Ranunculus karelinii S.K.Cherepanov, Sosud. Rast. SSSR, 425. 1981, nom. superfl. Type: In summis alpibus Alatau ad fontes fl. Lepsa, in glareosis ad scaturigines nivibus formatus deliquescentibus, 1841, Karelin et Kiriloff (isotype: NY - Torrey!)

Plant to 15 cm tall. Roots slender or fleshy, <1–2 mm thick. Leaves (margins and sometimes surfaces), stems, petioles and pedicels sparsely spreading-pubescent with long weak hairs. Basal leaves to 4–10 cm long, blade to 7–23 mm long, 12–25 mm wide, 3-foliolate, leaflets with well-defined petiolules; leaflets again 2–3-parted and the parts lobed, ultimate segments oblanceolate to obovate, 1–3 mm wide. Cauline leaves similar but shorter. Flowers solitary. Sepals 3–5 × 3–4 mm, spreading-pubescent with long weak hairs; petals 7–9 × 4.5–9 mm; receptacle pubescent. Achenes glabrous, 2.3 × 1.2 mm, very strongly asymmetrical (ventricose), beak 0.4 mm long, straight, inflexed so that it is ± perpendicular to axis of achene.

Alpine areas on stony soil and talus where watered by snowmelt. Endemic to the Jungarskiy Alatau and Tien Shan, Central Asia: Kazakhstan (Cherepanov 1995) and Xinjiang, China (Wang & Gilbert 2001).

Additional specimens examined: **KAZAKHSTAN:** Kumdaban, Jungar Mts., 9000 ft, May 1879, *A. Regel s.n.* (US). **CHINA. Xinjiang:** Tian Shan SW of Manas (W of Urumchi), on talus, 21 Jul 1957, *A.A. Yunatov, Li Shi-In, & Yuan Y-Fen 948* (MO).

ACKNOWLEDGMENTS

I would like to thank the curators of ALA, CAS, COLO, GH, MO, NY, UC, and US for providing specimen loans, facilities for work at their herbaria, or information on specimens in their collections, and Tom Zanoni for helpful discussions. Dave Murray and Bruce Ford provided useful comments on an earlier version of the manuscript.

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INFRAGENERIC TAXONOMY OF *ASTROPHYTUM* (CACTACEAE), WITH REMARKS ON THE STATUS OF *DIGITOSTIGMA*

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ABSTRACT

In a monograph of the genus *Astrophytum*, Megata (1944) proposed two infrageneric sections—*Astrophytum* sect. *Austrastrophytum* and *A.* sect. *Septentriastrophytum*. *Astrophytum* sect. *Austrastrophytum* which contains the type of the genus is in violation of Art. 22.2 of the ICBN which requires that a name of a subdivision of a genus that includes the type of that genus repeat as its epithet the generic name unaltered. Backeberg (1950) proposed two subgenera: *Astrophytum* subg. *Euastrophytum* and *A.* subg. *Neoastrophytum*, which essentially corresponded to Megata's sections. However, Backeberg's *A.* subg. *Euastrophytum*, containing the type species of the genus, violated Art. 22.2 and Art. 21.3 of the international code.

In 1961, Backeberg used *Astrophytum* subg. *Neoastrophytum* in his treatment of the genus, but proposed *Astrophytum* subg. *Astrophytum* to replace *A.* subg. *Euastrophytum*. Therefore, Backeberg's (1961) subgeneric names are valid, and have received wide circulation, and should be accepted; Megata's two sections should be suppressed. On the basis of comparative flower and fruit morphology, the species *Digitostigma caput-medusae* Velazco & Nevárez appears to have evolved within the genus *Astrophytum*, and shows a closer relationship to *A.* subg. *Neoastrophytum* than to *A.* subg. *Astrophytum*. However, because of its aberrant characteristics (tuberculate habit, dimorphic areoles, large, fusiform root, and nearly circular seeds with an acute basal cleft and verrucose testa), *caput-medusae*'s placement in *Astrophytum* subgenus *Stigmatodactylus* D. Hunt appears justified, though provisional, because its status as an ancient generic hybrid remains a possibility. Molecular genetic studies are needed to further clarify the evolutionary relationships of *A. caput-medusae*.

RESUMEN

En una monografía del género *Astrophytum*, Megata (1944) propuso dos secciones infragenéricas —*Astrophytum* sect. *Austrastrophytum* y *A.* sect. *Septentriastrophytum*. *Astrophytum* sect. *Austrastrophytum* que contiene el tipo del género viola el Art. 22.2 del ICBN que requiere que un nombre de una subdivisión de un género que incluya el tipo del género repite como epíteto el nombre genérico inalterado. Backeberg (1950) propuso dos subgéneros: *Astrophytum* subg. *Euastrophytum* y *A.* subg. *Neoastrophytum*, que esencialmente corresponden a las secciones de Megata. Sin embargo, *A.* subg. *Euastrophytum* Backeberg, contiene la especie tipo del género, y viola los Art. 22.2 y Art. 21.3 del Código international.

En 1961, Backeberg usó *Astrophytum* subg. *Neoastrophytum* en su tratamiento del género, pero propuso *Astrophytum* subg. *Astrophytum* para reemplazar *A.* subg. *Euastrophytum*. Por tanto, los nombres subgenéricos de Backeberg (1961) son válidos, han tenido amplia circulación, y deben ser aceptados; las dos secciones de Megata deben suprimirse. En base a la morfología comparativa de flor y fruto, la especie *Digitostigma caput-medusae* Velazco & Nevárez parece haber evolucionado en el género *Astrophytum*, y muestra una relación más grande con *A.* subg. *Neoastrophytum* que con *A.* subg. *Astrophytum*. Sin embargo, debido a sus características aberrantes (hábito tuberculado, areolas dimórficas, raíz ancha, fusiforme, y semillas casi circulares con una hendidura basal y testa verrucosa), el emplazamiento de *caput-medusae* en *Astrophytum* subgénero *Stigmatodactylus* D. Hunt parece justificado, aunque provisional, porque su estatus como un antiguo híbrido genérico es aún una posibilidad. Se necesitan estudios genéticos moleculares para clarificar las relaciones evolutivas de *A. caput-medusae*.

SUBGENUS VS. SECTION

The cactus genus *Astrophytum* comprises a small group of species occurring principally in the Chihuahuan Desert region of central and northern Mexico, with one species entering southern Texas (Anderson 2001; Hunt et al. 2006). On the basis of hybridization experiments involving the different species, Möller (1927) recognized two apparently natural groups within the genus. A decade later, the German horticulturalist, Curt Backeberg (1937), presented a brief, descriptive key to the species of *Astrophytum* in *Blätter für Kakteenforschung*, a bulletin of cactus research. He also recognized two groups within the genus—Group A having apical fruit dehiscence and yellow flowers, and Group B with basal fruit dehiscence and red-throated flowers.

Moritane[1] Megata, a student of horticultural sciences at the Kyoto Imperial University in Kyoto, Japan,

[1]**Moritane, not Molitane is the correct spelling of Megata's first name; see Hoock (2008, p. 248) for explanation.**

published the first monographic treatment of the genus *Astrophytum* in 1944. Data from experimental hybridization and comparative morphology, led him to propose two infrageneric sections—*Astrophytum* sect. *Septentriastrophytum* (diagnosis: *Flores floribus Sect. Austrastrophyti majores, aurea praeter intus basi rubra; fructus carnosus, irregulariter dehiscens; semina copiosa, 80–300, nigra vel luteobrunnescentia.*), and *A.* sect. *Austrastrophytum* (diagnosis: *Flores minores quam flores Sect. Septentriastrophyti, lutei et non rubric intus ad basim; fructus siccus, stellatim dehiscens; semina 40–60, nigra*). Megata recognized five species, placing *A. myriostigma* and *A. ornatum* in *A.* sect. *Austrastrophytum* and *A. asterias*, *A capricorne*, and *A. coahuilense* in *A.* sect. *Septentriastrophytum*.

In 1950, Curt Backeberg published two subgenera under *Astrophytum* which corresponded exactly to Megata's (1944) sections. He proposed *Astrophytum* subg. *Euastrophytum* (diagnosis: *Fauce lutea; fructu apice stellariter dissiliente*) with the type species *Astrophytum myriostigma* Lem. (1839) and *A.* subg. *Neoastrophytum* (diagnosis: *Fauce rubra; fructu basi dissiliente*), with the type species *Echinocactus asterias* Zuccarini (1845).

Backeberg's six volume series *Die Cactaceae* was published in 1958 to1962, and the genus *Astrophytum* was treated in his volume 5 (1961). Backeberg proposed *Astrophytum* subg. *Astrophytum* to replace *A.* subg. *Euastrophytum*, and adopted his previously published *A.* subg. *Neoastrophytum*. He apparently realized that *Astrophytum* subg. *Euastrophytum* violated Art. 22.2 of the ICBN which requires that a name of a subdivision of a genus that includes the type of that genus repeat as its epithet the generic name unaltered, and therefore this subdivision should have been named *Astrophytum* subg. *Astrophytum*. Furthermore, Art. 21.3 forbids the epithet of a subdivision of a genus to be formed from "Eu" plus the generic name. Backeberg separated the two subgenera on the basis of fruit morphology, type of fruit dehiscence, and seedling color. He recognized a total of six species, placing *A. myriostigma* and *A. ornatum* in *Astrophytum* subg. *Astrophytum*, and *A. asterias*, *A. capricorne*, *A. coahuilense*, and *A. senile* in *A.* subg. *Neoastrophytum*. He followed the same taxonomy in the first (1966), second (1970) and third (1976) editions of *Kakteenlexikon* (as well as the English version of the third edition, *Cactus Lexicon* 1977). However, he abbreviated the subgeneric diagnoses, using only the mode of fruit dehiscence as a diagnostic trait.

The fundamental dichotomy within the genus *Astrophytum* was also recognized by the *Astrophytum* specialist Otakar Sadovský who carried out long-term hybridization experiments involving hundreds of plants. However, he and his coauthors did not give formal taxonomic recognition, either at the level of section or subgenus, to these two clades (Haage & Sadovský 1957; Sadovský & Schütz 1979). More recent evidence from chloroplast DNA seems to further support this basic division within *Astrophytum* (Wallace 1995, Fig. 5).

As is evident from the foregoing discussion, essentially the same two groups of species in the genus *Astrophytum* have been treated in the past both as sections and as subgenera by two different authors, creating a taxonomic problem requiring resolution. Furthermore, this problem has persisted in recent works. In *The New Cactus Lexicon* (Hunt et al. 2006: 31), Backeberg's *Astrophytum* subg. *Astrophytum* and *A.* subg. *Neoastrophytum* are recognized as well as *A.* subg. *Stigmatodactylus* D. Hunt. By contrast, in a new monographic treatment of *Astrophytum*, Hoock (2008) allocates five species to Megata's (1944) sections, *A.* sect. *Austrastrophytum* and *A.* sect. *Septentriastrophytum*, and places a sixth species, *Astrophytum caput-medusae* (Velazco & Nevárez) D. Hunt, in *A.* subg. *Stigmatodactylus* D. Hunt, following Hunt (2003a, b).

The decision whether to divide a genus into sections or subgenera is subjective. In reviewing the question in this case, it appears that the use of the subgenus is more appropriate and justifiable than the use of the section for the following three reasons: 1) Megata's (1944) *A.* sect. *Austrastrophytum* is in violation of ICBN Art. 22.2 because this section includes the type (*Astrophytum myriostigma*) of the generic name; it should have been named *A.* sect. *Astrophytum*. 2) Backeberg's two subgeneric names, *A.* subg. *Astrophytum* and *A.* subg. *Neoastrophytum*, are validly published and have received wide circulation, appearing in volume 5 of his *Die Cactaceae* and in all three German editions of *Kakteenlexikon* as well as the English translation of his third edition. 3) Hunt (2003a, b) proposed *A.* subg. *Stigmatodactylus* to accommodate the morphologically divergent *A. caput-medusae*, thereby setting further precedence for the use of the subgenus category as opposed to the section, and as indicated above, the subgenus category was adopted in *The New Cactus Lexicon*.

STATUS OF *DIGITOSTIGMA*

Velazco and Nevárez (2002) described a new genus and species, *Digitostigma caput-medusae* from Nuevo León, Mexico. Subsequently, Hunt (2003a) wrote: "The authors of *Digitostigma caput-medusae* are to be congratulated on a truly remarkable discovery, but the feeling of our group is that its peculiar habit is not sufficient in itself to justify excluding it from *Astrophytum*, with which it shares unusual and significant features in common, i.e., the floccose indumentum and eccentric (hat-shaped) seeds, as well as having very similar flowers." Hunt (2003a) therefore placed *Digitostigma* in the synonymy of *Astrophytum* and recombined the species as *Astrophytum caput-medusae* D. Hunt.

Shortly thereafter, Hunt (2003b) wrote that Kanchi Gandhi of Harvard University had determined that Velazco and Nevárez "had failed to indicate the type of the generic plant in the explicit manner required for the ICBN," thus invalidating both the name *Digitostigma* and the species name. Gandhi regarded Hunt (2003a) as the valid publication of the name *Astrophytum caput-medusae* as well as the subgeneric name, *A.* subg. *Stigmatodactylus*. But according to Hunt (2003b), Nigel Taylor argued that Velazco and Nevárez had failed to provide a validating Latin diagnosis for the species name and therefore the original description and Hunt's revision were invalid. To correct this error, Hunt (2003b) published a second formal revision as follows:

"*Astrophytum caput-medusae* D. Hunt *ab aliis speciebus generic Astrophyti caule tuberculis elongates areolis bipartitis maxime differt*. Type: Mexico, edo. Nuevo León, [locality withheld], matorral espinoso tamaulipeco, 100–200 m, 28 Aug 2001, *Nevárez & Velazco s.n.* (UNL 023704 holo.; UNL 023705 iso.). Syn: *Digitostigma caput-medusae* Velazco & Nevárez, Cact. Suc. Mex. 47(4):81–82 (2002) nom inval. (Art. 43.1)."

"*Astrophytum* subg. *Stigmatodactylus* D. Hunt Replaced *Digitostigma* Velazco & Nevárez Cact. Suc. Mex. 47(4):79 (2002) nom inval. (Art. 37.5), quoad descr. Lat. Type: *Astrophytum caput-medusae* D. Hunt."

Then in the editorial section of *Cactaceae Systematics Initiatives* 20:4. 2005, we are informed that Roberto Kiesling and Detlev Metzing proposed a clause to ICBN Art. 37, that was approved by the International Botanical Congress in Vienna (July 2005). The clause removes the "pitfall" introduced when said Article was previously amended in 1990 which invalidated the generic name *Digitostigma* Velazco & Nevárez when originally published, as well as the specific names *D. caput-medusae* Velazco & Nevárez and *Astrophytum caput-medusae* (Velazco & Nevárez) D. Hunt. The draft Art. 37.7 states: "In the case of a new monotypic genus (or monotypic infrageneric taxon above the rank of species), the correct mention of, or reference to, the type of the species name is sufficient." As a result of the acceptance of the clause to Art. 37, the original names in *Cactaceas y Suculentas Mexicanas* 47(4):76–86. 2002, and the recombination in *Astrophytum* (*Cactaceae Systematics Initiatives* 15:6. 2003a) retroactively became validly published, and the "validation" of *A. caput-medusae* (*Cactaceae Systematics Initiatives* 16:4. 2003b) was judged superfluous. Consequently, if authors prefer to classify the new taxon as a distinct genus, the correct name would be *Digitostigma caput-medusae* Velazco & Nevárez. But if it is to be regarded as a member of *Astrophytum*, then the correct name would be *Astrophytum* subg. *Stigmatodactylus caput-medusae* (Velazco & Nevárez) D. Hunt, and *Digitostigma* would be placed in the synonymy of *Astrophytum*.

Detailed morphological comparisons between *caput-medusae* and *Astrophytum* have been lacking until now. In an attempt to clarify *caput-medusae*'s affinities and generic status, a summary of my comparative study is presented below. Flowers, fruits, and seedlings of the following taxa were examined (number of flowers, fruits, adult plants, and seedlings in parentheses): *A. ornatum* (3, 3, 2, 69), *A. myriostigma* (22, 41, 41, 249), *A. asterias* (29, 5, 5, 59), *A. capricorne* (40, 11, 14, 82), *A. coahuilense* (16, 20, 20, 120), and the species *caput-medusae* (34, 8, 5, 14).

The flower of *caput-medusae* has a vivid orange color at the base of the inner perianth segments (Velazco & Nevárez 2002) and in this respect it is similar to that of *A.* subg. *Neoastrophytum* species in which the inner perianth segments vary from crimson to orange. By contrast, members of *A.* subg. *Astrophytum* have entirely yellow flowers. The fruit of *A.* subg. *Neoastrophytum* is described as fleshy and turns pink, red, or reddish purple when ripe, whereas that of *A.* subg. *Astrophytum* is less fleshy and remains green (Megata 1944; Hoock 2008). The fruit of *caput-medusae* is similar to that of *A.* subg. *Neoastrophytum* in that it usually

turns pink at maturity (Hoock 2008); but at maturity it appears less fleshy to nearly dry and in this respect is similar to the fruit of *A.* subg. *Astrophytum*. The fruit of *caput-medusae* undergoes longitudinal dehiscence (Velazco & Nevárez 2002) and hence differs from both *Astrophytum* subgenera. According to Velazco and Nevárez (2002:82), the remains of the perianth are deciduous and leave a 3 mm diameter scar. However, in all fruit that I observed the floral remnants persisted until dehiscence. In *A.* subg. *Neoastrophytum* the floral remnants are strongly attached to the fruit, but in *A.* subg. *Astrophytum* they usually detach from the fruit at the time of dehiscence, leaving a small scar.

The flower and fruit of *caput-medusae* display similarities in particular with those of *Astrophytum asterias*. In both taxa, the exterior perianth segments are greenish-yellow and they usually lack, or have few, black tips. In *A.* subg. *Neoastrophytum capricorne* and *A.* subg. *Neoastrophytum coahuilense* the exterior perianth segments are usually yellow with black tips, and often there is a reddish line or spot near each black tip. The bases of the inner perianth segments in *caput-medusae* are vivid orange; in *A. asterias* the color may vary from dark red to pink or orange. In *A. capricorne* and *A. coahuilense*, the bases of the inner perianth segments are usually dark crimson, but may vary from pale red to orange, or rarely, pure yellow in natural populations (Hoock 2008). In *A. asterias* the mature fruit turns pink (Hoock 2008; this study) like that of *caput-medusae*. Furthermore, in *caput-medusae*, the receptacle tube and pericarpel are covered with fewer lanceolate scales and more white wool than in the species of both *Astrophytum* subgenera, except in *A. asterias* which displays a further reduction in number and size of these scales (i.e., spinescent bracteoles) and more wool, especially on the pericarpel.

Velazco and Nevárez (2002) stated that the seeds of *D. caput-medusae* are "hat-shaped" and compare favorably with those of *Astrophytum*, and according to Hunt (2003a) they resemble those of *A. asterias*. However, my study suggests that the seeds of all *Astrophytum* species are very similar to one another and differ collectively from those of *D. caput-medusae* in several ways. The seeds of all *Astrophytum* species have a smooth testa whereas those of *D. caput-medusae* are verrucose (Velazco & Nevárez 2002). The seeds of *Astrophytum* clearly fit the concept of "hat-shaped," with a peaked, but rounded profile opposite the hilum and a rather flat base (where the concavity of the hilum is situated). But the seeds of *caput-medusae* have a deeply and acutely angled cleft at the concavity of the hilum and the lateral profile opposite the hilum is especially enlarged and rounded.

The seedlings of *caput-medusae* are usually light green, but they can be dark violet in color. Seedlings of all members of *A.* subg. *Neoastrophytum* are typically light green, whereas those of *A.* subg. *Astrophytum* are generally russet or reddish brown, rarely green.

The distributional relationships of the taxa under consideration are also informative. *Astrophytum* subg. *Astrophytum* has a southerly distribution with *A. myriostigma* centered on the plateau of San Luis Potosi and adjacent areas including the Jaumave Valley, and *A. ornatum* occurring through the barranca region as far south as the state of Hidalgo (Megata 1944; Hoock 2008). On the other hand, *A.* subg. *Neoastrophytum* has a northerly distribution, ranging from extreme northern Zacatecas and adjacent Durango, northward and eastward through Coahuila and adjacent Nuevo León into southern Texas (Hoock 2008). The species *caput-medusae* also has a northern distribution, being restricted to northern Nuevo León (Velazco & Nevárez 2002) adjacent to the range of *A. capricorne* and *A. asterias*.

In sum, comparative data from flower and fruit characteristics, and seedling color support the hypothesis that *caput-medusae* is a member of the genus *Astrophytum*. Moreover, the evidence (including geographic relationships) suggests that *caput-medusae* is more closely related to *A.* subg. *Neoastrophytum* than to *A.* subg. *Astrophytum* and may have evolved from the former group after it had separated from the latter. Therefore, accepting *Digitostigma* as a distinct genus to accommodate *caput-medusae* would render the genus *Astrophytum* a paraphyletic taxon, which would be undesirable in a classification system based on phylogenetic principles. It is clear, however, that *caput-medusae* has undergone considerable morphological divergence from the other *Astrophytum* species, possibly as a result of strong selection pressures for adaptation to the Tamaulipan thornscrub habitat, perhaps as a shrub debris mimic.

As an alternative hypothesis, the remarkable divergence resulting in the unusual suite of morphological characteristics (tuberculate habit, dimorphic areoles, large, fusiform root, and large rounded seeds with a verrucose testa and acute basal cleft) could be explained by intergeneric hybridization, a possibility previously raised by Hunt (2003a). If true, separate generic status for *caput-medusae* would then be justified. If *caput-medusae* is an ancient hybrid, it is reasonable to assume that a member of *A.* subg. *Neoastrophytum* was involved as one of its parents. The other parent could have had a pure yellow flower. One characteristic of the flower of *caput-medusae* that suggests hybridization is the narrowness of zone of orange color surrounding the stamens. A narrow zone of color is typical of *Astrophytum* hybrids produced artificially by crossing a pure yellow-flowered species (e.g., *A. myriostigma*) with a species with red-throated flowers (e.g., *A. capricorne*, *A. asterias*); see Hoock (2008) for examples. Without doubt, molecular genetic studies are needed to further clarify the evolutionary relationships of *caput-medusae*.

CONCLUSIONS

It is recommended that *A.* sect. *Austrastrophytum* Megata nom. inval., (Art. 22.2), and *A.* sect *Septentriastrophytum* Megata should be suppressed. Backeberg's *Astrophytum* subg. *Astrophytum* and *A.* subg. *Neoastrophytum* should be accepted and used when necessary. The species *Digitostigma caput-medusae* Velazco & Nevárez appears to have evolved within the genus *Astrophytum*, and shows a closer relationship to *A.* subg. *Neoastrophytum* than to *A.* subg. *Astrophytum*. However, because of its aberrant morphology, *caput-medusae*'s placement in *A.* subg. *Stigmatodactylus* D. Hunt appears justified, though provisional; its status as an ancient intergeneric hybrid remains a possibility. Molecular genetic studies are needed to resolve this question. Protologues and a diagnostic key to the three subgenera follow:

Astrophytum subg. **Astrophytum** Backebg., Die Cactaceae 5:2655, fig. 2526. 1961. Subg. *Euastrophytum* Backebg., Cac. Succ. J. (Los Angeles) 22:5. 154. 1950. Type species: *Astrophytum myriostigma* Lem., Cact. Gen. Sp. Nov. 4(-6). 1839. Type locality: not cited.

Diagnosis.—Fauce lutea; fructu apice stellariter dissiliente. *Distribution*.—North-central Mexico (Backeberg 1950:154).
Diagnosis.—Frucht sternformig aufspringend, mit festerer Wand, Samlinge rotbraun (Backeberg 1961:2653).
Note.—Distribution is central Mexico, not north-central Mexico.

Astrophytum subg. **Neoastrophytum** Backebg., Cac. Succ. J. (Los Angeles) 22:5. 154. 1950. Type species: *Echinocactus asterias* Zucc., Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 4(2):13, t. 3. 1845. Type Locality: Mexico.

Diagnosis.—Fauce rubra; fructu basi dissiliente. *Distribution*.—Central Mexico.
Note.—Distribution is north-central Mexico, not central Mexico.

Astrophytum subg. **Stigmatodactylus** D. Hunt, Cactaceae Syst. Init. 15:6. 2003. Replaced synonym: *Digitostigma* Velazco & Nevárez, Cact. Succ. Mex. 47:79. 2002. Type: *Digitostigma caput-medusae* Velazco & Nevárez, Cact. Suc. Mex. 47:81–82.

'*Digitostigma*' not only contravenes Linnaean canons for the formation of generic names but implies that the plant is notable for its finger-shaped stigmas rather than its spotted tubercles, contrary to the authors' explicit intention. For this reason the opportunity afforded by the change of rank has been taken to provide an unambiguous name formed according to classical usage.

Astrophytum caput-medusae (Velazco & Nevárez) D. Hunt, Cactaceae Syst. Init. 15:6. 2003. *Digitostigma caput-medusae* Velazco & Nevárez, Cact. Suc. Mex. 47:81–82. Type: MEXICO. Nuevo León: [locality withheld], matorral espinoso tamaulipeco, 100–200 m, 28 Aug 2001, *Nevárez & Velazco s.n.* (holotype: UNL 023704; isotype: UNL 023705).

Diagnosis.—Radix fusiformis radices secundarians edens, pro ratione plantae parte aerea magna. Caulis brevis, cylyndraceus, costas carens, tuberculis longissimis gecilibus ex caulis apice orientibus, epiderme stigmatis obtecta. Spinae plerumque adsunt, in radiales vel centrales non differentes, breves, non perfecte rectae, aliquantum undulatae, albidae, ad apiceum atrocastaneae. Areolae dimorphae: spinifera ad tuberculi apicem, albolanata, circularis; florifera adaxialis, in tuberculi parte subterminali, a spinifera disjuncta. Flores in tuberculorum parte subterminali evolventium, non apicales, diurni, flavi, peranthi segmentis interioribus base aurantiaca, segmentis exterioribus flavo-viridibus; tubo receptaculari squamis lanceolatis, papiraceis, arista terminali obtecto, in quorum axillis pilis brevibus albis parientibus; pericarpello isdem squamis munito. Fructos juvenis viridis, carnosus, squamis lanceolatis ad axillis lanatis, ad maturitate sicco, dehiscentia longitudinali irregulari. Semina magna (Astrophyti similia), ad 3 mm longa, pileata, testa tuberculata, nigra vel atrobrunnea; hilo basali profundissimo, micropyle ab hilo externo, sed ad id contiguo (Velazco & Nevárez 2002:79).

KEY TO SUBGENERA

1. Fruits remain green, open apically; flowers yellow ________ subg. **Astrophytum** Backebg. (*A. myriostigma, A ornatum*)
1. Fruits turn pink, red or red-purple when ripe, split basally in circular fashion, disintegrate basally, or split longitudinally in irregular manner; flowers yellow usually with orange or red throat.
   2. Body with ribs________________ subg. **Neoastrophytum** Backebg. (*A. asterias, A capricorne, A. coahuilense*)
   2. Body with elongate tubercles________________ subg. **Stigmatodactylus** D. Hunt (*A. caput-medusae*)

ACKNOWLEDGMENTS

I wish to thank Nicholas J. Turland of the Missouri Botanical Garden for clarifications of the pertinent articles of the ICBN. I also thank A. Michael Powell for reading and commenting on a previous draft of this manuscript. Urs Eggli (ZSS) and an anonymous reviewer provided helpful reviews. Detailed photographs of live specimens and herbarium preparations of *Astrophytum caput-medusae* were obtained from Heinz Hoock and George Hinton, respectively.

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MYCOLOGICAL LITERATURE ON TEXAS FLESHY BASIDIOMYCOTA, TWO NEW COMBINATIONS, AND NEW FUNGAL RECORDS FOR TEXAS

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ABSTRACT

An extensive literature search was made to determine all published articles and new species or infraspecific taxa of fleshy basidiomycetous fungi described from Texas. This search resulted in 202 articles on Texas fungi with 89 new taxa described from Texas. We also report on 52 new records of fleshy basidiomycetous fungi from Texas and propose two new combinations, **Hygrocybe chamaeleon** and **Hygrocybe mississippiensis.**

RESUMEN

Se realizó una búsqueda extensa de todos los artículos publicados, de las especies nuevas, o taxa infraespecíficos de los hongos carnosos basidiomicetos descritos para Texas. Esta búsqueda dio como resultado 202 artículos relacionados con hongos en los que se describen 89 nuevos taxa para Texas por primera vez. También, reportamos aquí 52 nuevas especies de hongos carnosos basidiomicetos para Texas, y a la vez proponemos dos nuevas combinaciones **Hygrocybe chamaeleon** e **Hygrocybe mississippiensis.**

PART I—MYCOLOGICAL LITERATURE ON TEXAS FLESHY BASIDIOMYCOTA

David Lewis has been collecting fungi in southeast Texas for over 30 years. During this time he has attempted to amass the literature that documents the fleshy Basidiomycota throughout Texas. Reported here are the results of the literature search as conducted by both authors. The authors' primary research interests center around gilled mushrooms and boletes (Agaricales sensu lato – but see Part III of this paper for a newer classification) so perhaps the list below is most complete for the fungi of these groups. We have, however, attempted to locate references for other fleshy basidiomycetous fungi.

For a reference to be included in the list, a collection must be cited from Texas. For modern references this is not difficult to discern because of the exacting requirements of locality information and herbarium designations. Publications that give the distribution as "as far as Texas" or something similar without documentation of collections are not included. A little more liberty is yielded to the literature of the nineteenth or early twentieth centuries where geographic information might not be as complete, nor is there a guarantee that a herbarium specimen exists.

Following each reference is a number in parenthesis. The number indicates how many species, with at least one Texas record, are reported in the article. For taxa that have the holotype from Texas, the binomials and localities (sometimes only the state name was given in the protologue) where collected are provided beneath the references, followed by the herbarium location of the holotype. We have relied on literature references and online herbaria data to determine the location of the holotypes, but we have not confirmed their continued existence in the designated herbaria. For a few of the older taxa we were not able to determine the location of the types. We are aware that a number of the newly described taxa have since been nomenclaturally or taxonomically synonymized, but we feel that for the purposes of this paper it is best to give only the basionym as the starting reference.

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Boletus silvaticus Thiers (HOLOTYPE: TEXAS. Grimes Co.: Navasota; MICH)

Cystoderma texensis Thiers (HOLOTYPE: TEXAS. Montgomery Co.: Richards; MICH)

Lactarius albolutescens Thiers. (HOLOTYPE: TEXAS. Montgomery Co.: Richards; MICH)

Lactarius albus Thiers (HOLOTYPE: TEXAS. Walker Co.: Huntsville; MICH)

Lactarius cystidiosus Thiers (HOLOTYPE: TEXAS. San Jacinto Co.: Stubblefield Lake; MICH)

Lactarius eburneus Thiers (HOLOTYPE: TEXAS. Walker Co.: Huntsville; MICH)

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Marasmius puniceus Thiers (HOLOTYPE: TEXAS. Brazos Co.: Millican; MICH)

Melanoleuca reai var. *texana* Thiers var. nov. (HOLOTYPE: TEXAS. Brazos Co.: College Station; MICH)

Mycena radicata Thiers (HOLOTYPE: TEXAS. Montgomery Co.: Richards; MICH)

Mycena avellaneibrunnea Thiers (HOLOTYPE: TEXAS. San Jacinto Co.: Coldspring; MICH)

Mycena epipterygia var. *caespitosa* Thiers var. nov. (HOLOTYPE: TEXAS. Montgomery Co.: Richards; MICH)

Rhodophyllus verrucosus Thiers (HOLOTYPE: TEXAS. Brazos Co.: Wellborn; MICH)

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Conocybe antipoda var. *humicola* Thiers var. nov. (HOLOTYPE: TEXAS. Brazos Co.: Wellborn; MICH)

Coprinus comatus var. *texensis* Thiers var. nov. (HOLOTYPE; TEXAS. Montgomery Co.: near San Jacinto River; MICH)

Coprinus subangularis Thiers (HOLOTYPE: TEXAS. Montgomery Co.: Richards; MICH)

Coprinus subcurtus Thiers (HOLOTYPE: TEXAS. Brazos Co.: Millican; MICH)

Cortinarius acystidiosus Thiers (HOLOTYPE: TEXAS. San Jacinto Co.: Coldspring; MICH)

Cortinarius paliformis Thiers. (HOLOTYPE: TEXAS. Walker Co.: Huntsville; MICH)

Galerina autumnalis f. *robusta* Thiers f. nov. (HOLOTYPE: TEXAS. Montgomery Co.: Richards; MICH)

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DISCUSSION

We fear and predict that we have missed references for Texas because distribution reports are often found in obscure journals. We welcome feedback on citations that we may have missed and it is anticipated that a follow-up article with updated references will likely be forthcoming.

In addition to technical articles where collections are cited, there is additional literature in the format of field guides that include fungi found in Texas. Important is the field guide by Metzler and Metzler (1992) which includes 202 species primarily from southeastern Texas. Other useful field guides for the area include those by Bessette et al. (2000), Bessette et al. (2007), Horn et al. (1993), Lincoff (1981), Phillips (2005) and Weber and Smith (1985).

PART II—NEW COMBINATIONS

The following two combinations are proposed in accordance with modern generic concepts based on morphology (Singer 1986) and supported by molecular evidence (Matheny 2006). During the process of preparing this manuscript and checking information in the protologue (Cibula 1979) for *Hygrophorus chamaeleon*, it came to our attention that the information regarding the type designation was not in order. In the protologue, the type collection information for *chamaeleon* was cited as follows:

"Specimen typicum Cibula n. 589 in Herb. Mass conservatum est; legit prope Saucier, MS, 8 August 1974."

The first thing noticed was that the date for 589 was inconsistent with other numbers in the 500's for collections cited in the Materials Studied, and 589 was not again cited in the Materials Studied. Checking no. 589 in Cibula's field record book, which we have, 589 is listed as a *Russula*, and the date of that collection is 9 Oct. 1975. No *Hygrophorus* species were collected on that date. Unfortunately, we have not been able to confirm the whereabouts of 589 if it still exists as a collection. Checking the other collection numbers from Materials Studied of *chamaeleon* in Cibula's record book, he has "type" written next to coll. no. 489 and 489 is also cited in the Materials Studied. Upon examination of collection no. 489, "type spec." is written on the associated hand-written field label. The field label, record book and the original 5 × 8 in card with macroscopic description and collecting data all give the date for no. 489 as 20 Aug. 1974. Based on evidence from the field book and field label, Cibula had intended to designate 489 as the holotype, but somehow mistyped the collection information and date in the Latin description. We can find no violation of any articles in the International Code of Botanical Nomenclature (McNeill et al. 2006) for this error. We correct this error and conclude that Cibula coll. no. 489 is the holotype. Given below are the new combinations including the corrected type information for *H. chamaeleon.*

Hygrocybe chamaeleon (Cibula) Lewis & Ovrebo, comb. nov. BASIONYM: *Hygrophorus chamaeleon* Cibula, Mycotaxon 10:109. 1979. HOLOTYPE: MISSISSIPPI. HARRISON CO.: Saucier, Harrison Experimental Forest, De Soto National Forest, in humus along broadleaf evergreen draw across from Block II Plot 1, loblolly pine (north of plot), Fertilization Study Plots, 20 Aug 1974, *W.G. Cibula 489* (NY!).

Hygrocybe mississippiensis (Cibula) Lewis & Ovrebo, comb. nov. BASIONYM: *Hygrophorus mississippiensis* Cibula, Mycotaxon 10:106. 1979. HOLOTYPE: MISSISSIPPI. HARRISON CO.: Saucier, Harrison Experimental Forest, De Soto National Forest, on a raised mound of earth and stumps, and in leaf litter in mixed bottomland hardwoods, adjacent to Block IV, Plot 4, loblolly pine, Fertilization Study Plots, 8 Aug 1974, *W.G. Cibula 485* (NY!).

The field label gives the habitat for *H. mississippiensis* as a mixed pine/hardwood ravine. *Hygrocybe mississippiensis* was previously

reported from Texas (Lewis & Cibula 2000). The holotype collections of *H. chamaeleon* and *H. mississippiensis* were originally deposited at MASS, they are now at NY.

PART III—NEW RECORDS OF FLESHY FUNGI FOR TEXAS

The following records are a result of long-term efforts by D.P Lewis and C.L. Ovrebo of documenting the mycota of southeast Texas, through organized amateur and professional forays, and individual outings. This listing represents only a small beginning to the updating of fungus records for Texas and reflects only collecting done in southeast Texas. As is the case with all biodiversity studies, knowledge of the biodiversity of a region is a function of the efforts that have been mounted to conduct field work, and importantly, records must be based on vouchered collections. With the exception of the researches of Harry Thiers and David Lewis, no other mycologists have devoted equally the time and effort in cataloguing in a scientific way the fleshy mycota for this region. For this reason, our knowledge of the diversity of fungi for southeast Texas, let alone the entire state of Texas, is far from complete.

The orders and families listed below may not be the ones readers are most familiar with. Until recent years, families of mushrooms and boletes were included in the Agaricales (see Singer 1986). The order and family circumscriptions have changed significantly as a result of recent phylogenetic molecular analyses and now mushroom–type fungi and other fleshy fungi maybe placed in different orders and families to reflect a more natural classification system. Most of the classification hierarchy below is taken from Matheny et al. (2006) and the reader is directed to that entire Mycologia issue devoted to recent developments in elucidating our understanding of phylogenies of fungi.

BASIDIOMYCOTA: AGARICOMYCETES: AGARICALES

AGARICACEAE

Agaricus argenteus Braendle in Peck. Found on lawns.

Voucher specimen: **Galveston Co.:** Santa Fe, Santa Fe Independent School grounds, field at corner of 6th Street and Warpath Street, N 29° 23.049', W 95° 06.383', 24 Jan 2008, *DPL-8493* (F).

Agaricus pocillator Murr. Found in mixed pine-hardwood forest.

Voucher specimens: **Hardin Co.**: Big Thicket National Preserve, Jack Gore Baygall Unit, off FM 2937, 9 Nov 2002, *DPL-6647* (F). **Orange Co.:** Vidor, near 455 Virginia Lane, 15 Jan 1989, *DPL-4232* (F).

CORTINARIACEAE

Cortinarius aureifolius Peck. Found in an arid sandyland with *Pinus palustris* and oaks. (**Fig. 1**).

Voucher specimens: **Newton Co.:** Lewis Chapel community, Sand Ridge Cemetery, CR 4045, N 30° 44.580', W 93° 46.127', 19 Dec 2007, *Ovrebo 4718 & 4719* (CSU).

Cortinarius corrugatus Peck. Under *Quercus laurifolia* and in beech-oak forest.

Voucher specimens: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 19 Oct 2004, *DPL-6959* (F). Mayflower, Canyon Rim Nature Trail, N 31° 06.927', W 93° 43.752', 27 Oct 2004, *DPL-7049* (F); 29 Jul 2005, *DPL-7286* (F).

Cortinarius hesleri Ammirati & A.H. Smith. Found in hardwood bottomland and oak-hickory forests.

Voucher specimens: **Newton Co.:** Toledo-Bend, Sam Forse Collins Recreational Area, N 31° 10.029', W 93° 34.620', 20 Jul 2007, *DPL-8129* (F). **Tyler Co.:** Big Thicket National Preserve: Neches River Corridor Unit, Round Lake area, 13 Sep 2003, *DPL-6807* (F).

Cortinarius violaceus (L.) S.F. Gray. Found in older pine forests.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Turkey Creek Unit, Kirby Nature Trail, 3 Dec 1978, *DPL-1670* (F); Jack Gore Baygall Unit, Arco Oil Field Road, 28 Nov 1980, *DPL-2451* (F); Jack Gore Baygall Unit, near FM 2937, 30 October 1993, *DPL-5092* (F); 9 Nov 2002, *DPL-6645* (F); 27 Nov 2004, *DPL-7104* (F); Saratoga, Lance Rosier Unit, Teel Road, N 30° 15.629', W 94° 31.532', 7 Nov 2006, *DPL-7608* (TAES); 11 Nov 2006, *DPL-7643* (TAES). **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy. 87, N 30° 42.509', W 93° 49.630', 1 Nov 1997, *DPL-5962* (F).

ENTOLOMATACEAE

Clitopilus prunulus (Scop.) P. Kumm. Found in floodplains, oak and pine forest.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Saratoga, Lance Rosier Unit, Cotton Road, 10 Jul 1988, *DPL-4135* (F). **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 10 Jun 2001, *DPL-6459* (F); 18 Jun 2003, *DPL-6687* (F); 12 Sep 2007, *DPL-8274* (F).

Clitopilus hobsonii (Berk. & Br.) P.D. Orton. Found on rotten wood. Previously known from Europe, Florida and North Carolina.

Voucher specimen: **Hardin Co.:** Silsbee, residence on Pine Street, 31 Jul 1988, *DPL-4163* (F).

Entoloma megacystidiosum Hesler. Found in mixed pine-hardwood and beech forests, previously known only from the type in Tennessee.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Lance Rosier Unit, Saratoga. Cotton Road, 13 Jun 2007, *DPL-7906* (F); Turkey Creek Unit, Kirby Nature Trail, 22 Jul 2007, *DPL-8141* (F). **Newton Co.:** Mayflower, Canyon Rim Nature Trail, N 31° 06.927', W 93° 43.752', 3 Jul 2007, *DPL-8084* (F); 20 Jul 2007, *DPL-8122* (F).

HYGROPHORACEAE

Hygrocybe chamaeleon (Cibula) Lewis & Ovrebo. Found in moss and mixed pine and hardwood forests, previously known from Harrison Co., Mississippi. (**Fig. 3**).

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Saratoga, Lance Rosier Unit, Cotton Road, 13 Jun 2007, *DPL-7911* (F); Turkey Creek Unit, Kirby Nature Trail, 22 Jul 2007, *DPL-8142* (F).

Hygrophorus borealis f. **salmoneus** Coker. Known only from the type in North Carolina. Found in an upland pine forest next to *Magnolia grandifolia*.

Voucher specimen: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 24 Nov 2008, *DPL-8815* (F).

Hygrophorus caespitosus (Murr.) Murr. Found in hardwood forests.

Voucher specimens: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 28 Jun 2003, *DPL-6716* (F); 5 Jul 2003, *DPL-6742* (F). **Tyler Co.:** Temple-Inland Forest Lake Experimental Forest, *Quercus alba* test plot 26 Jun 1994, *DPL-5305* (F).

Hygrophorus hypothejus (Fr.) Fr. Found with *Pinus taeda*.

Voucher Specimens: **Jasper Co.:** Buna, Temple-Inland Black Branch Hunting Club, off CR 701 and FM 1004, 24 Dec 1991, *DPL-4578* (F). **Newton Co.:** Lewis Chapel Community, Sand Ridge Cemetery, CR 4045, 30 Dec 2006, *DPL-7798* (F). **Tyler Co.:** Big Thicket National Preserve, Turkey Creek Unit, Muscadine Road, 15 Dec 1979, *DPL-2147* (F).

Hygrophorus perplexus A.H. Smith & Hesler. Found in mixed pine and hardwoods.

Voucher specimen: **Hardin Co.:** Big Thicket National Preserve, Saratoga, Lance Rosier Unit, Teel Road, N 30° 15.629', W 94° 31.532', 11 Nov 2006, *DPL-7623* (TAES).

HYMENOGASTRACEAE

Hebeloma sarcophyllum (Peck) Sacc. Found with *Quercus alba* and mixed pine-hardwood forests.

Voucher specimens: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 13 May 2000, *DPL-6265* (F). **Tyler Co.:** Temple-Inland Forest Lake Experimental Forest, *Quercus alba* test plot, 15 Jun 1994, *DPL-5258* (F).

Hebeloma sinapizans (Fr.) Sacc. Found in mixed pine and hardwood forests.

Voucher specimens: **Newton Co.:** Lewis Chapel community, Sand Ridge Cemetery Road, CR 4045, near cemetery, N 30° 44.572', W 93° 46.094', 21 Dec 2007, *DPL-8438* (F). **Tyler Co.:** Big Thicket National Preserve: Canyonlands Unit, near Spurger, N 30° 43.241', W 94° 08.404', 20 Dec 2007, *DPL-8463, DPL-8464* (F).

LYOPHYLLACEAE

Tephrocybe palustris (Peck) Donk. Found in sphagnum moss.

Voucher specimens: **Orange Co.:** Vidor, near Virginia Lane, 10 May 1979, *DPL-1724, DPL-1725* (F); 22 Feb 1986, *DPL-3954* (F); 28 Feb 1990, *DPL-4355* (F).

MARASMIACEAE

Marasmius fulvoferrugineus Gilliam. Found in leaf litter.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Lance Rosier Unit, Saratoga, Teel Rd, N 30° 15.629', W 94° 31.532', 11 Nov 2006, *DPL-7681* (TAES); 19 Jul 2007, *DPL-8107* (F); Turkey Creek Unit, Kirby Nature Trail, 16 Jun 2007, *DPL-7989* (F). **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 20 Nov 2004, *DPL-7092* (F).

OMPHALOTACEAE

Gymnopus luxurians (Peck) Murr. Subcaespitose on pine mulch.

Voucher specimen: **Jefferson Co.:** Beaumont, campus of Lamar University near John Gray Institute, 10 Jul 2006, *DPL-7494* (F).

PLUTEACEAE

Volvariella pusilla (Pers.) Sing. Found on soil, with mixed pine and hardwoods.

Voucher specimen: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 31 Aug 2003, *DPL-6770* (F).

Volvariella taylori (Berk. & Br.) Sing. Found in a dried up cypress swamp.

Voucher specimen: **Hardin Co.:** Big Thicket National Preserve, Saratoga, Lance Rosier Unit, Teel Road, N 30° 15.629', W 94° 31.532', 17 Jun 2006, *DPL-7422* (F).

PSATHYRELLACEAE

Psathyrella rugocephala (G.F. Atk.) A.H. Smith. Found in a hardwood forests.

Voucher specimens: **Fort Bend Co.:** Brazos Bend State Park, Hale Lake Nature Trail, 18 Nov 2006, *DPL-7759* (F, TAES).

Psathyrella carbonicola A.H. Smith. Reported from the western U.S. and Michigan. On burned ground.

Voucher specimen: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 27 Nov 2008, *DPL-8818* (F).

STROPHARIACEAE

Hypholoma sublateritium (Fr.) Quél. Found on a well decayed hardwood stump.

Voucher specimen: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 28 Nov 2008, *DPL-8823* (F)

Phaeomarasmius curcuma (B. & C.) Sing. Found on wood (**Fig. 2**).

Voucher specimens: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 24 Dec 1999, *DPL-6214* (F); 21 Nov 2007, *Ovrebo 4706* (CSU). **Orange Co.:** Vidor, near 455 Virginia Lane, 12 Apr 1977, *DPL-915* (F); 14 May 1977, *DPL-949* (F); 17 May 1977, *DPL-955* (F); 23 May 1977, *DPL-973* (F); 21 Apr 1978, *DPL-1361* (F); 4 May 1978, *DPL-1372* (F); 29 Dec 1981, *DPL-2856* (F).

Psilocybe caerulescens Murr. Found in a *Pinus* plantation. Known from Alabama, central Mexico, Venezuela and Brazil.

Voucher specimen: **Tyler Co.:** Big Thicket National Preserve, Spurger, in pine plantation near Neches River Corridor Unit, 13 Sep 2003, *DPL-6800* (F, XAL).

TRICHOLOMATACEAE

Clitocybe trulliformis (Fr.) P. Karst. Found in pine duff.

Voucher Specimen: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 28 Jan 2001, *DPL-6400* (F).

Tricholoma niveipes Peck. Found in arid sandy soil with pines and oaks (**Fig. 4**).

Voucher specimens: **Newton Co.:** Lewis Chapel Community, Sand Ridge Cemetery, CR 4045, N 30° 44.572', W 93° 46.094', 30 Dec 2006, *Ovrebo 4637* & 21 Dec 2007, *Ovrebo 4731* (CSU). (Fig. 4)

BOLETALES

Boletellus chrysenteroides (Snell) Sing. Found in mixed pine-hardwood forests.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Turkey Creek Unit, Kirby Nature Trail, Big 19 Sep 1980, *DPL-2314* (F); Jack Gore Baygall Unit, off FM 2937, 4 Jul 1981, *DPL-2664* (F); Lance Rosier Unit, Cotton Road, near Saratoga, 28 May 1984, *DPL-3656* (F); 5 Aug 1984, *DPL-3697* (F). **Tyler Co.:** Big Thicket National Preserve, Beech Creek Unit, Nature Trail, 4 Aug 1982, *DPL-3241* (F); Spurger, near Neches River, 10 Aug 1982, *DPL-3276* (F).

Boletus auripes Peck. Found with *Quercus alba*, *Quercus falcata* var. *leucophylla*, *Quercus nigra* and other oaks.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Jack Gore Baygall Unit, off FM 2937, 16 Aug 1982, *DPL-3328* (F); Saratoga, Lance Rosier Unit, Cotton Road, 5 Aug 1984, *DPL-3700* (F). **Tyler Co.:** Temple-Inland Forest Lake Experimental Forest, Sawtooth oak (*Quercus* sp.) test plot, 9 Jun 1992, *DPL-4635* (F); *Quercus alba* test plot, 12 Jun 1992, *DPL-4636* (F); *Quercus falcata* var. *leucophylla* test plot, 21 Jun 1992, *DPL-4699* (F); *Quercus nigra* test plot, 7 Jun 1997, *DPL-5783* (F).

Boletus hortonii A.H. Smith & Thiers. Found in stream floodplain forest.

Voucher specimen: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 1 Jul 1996, *DPL-5672* (F).

Boletus hypocarycinus Sing. Found in floodplains, oak and pine forest.

Voucher specimens: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 19 Oct 2004, *DPL-6966* (F). Lewis Chapel community, Sand Ridge Cemetery Road, CR 4045, 12 Jul 2006, *DPL-7519* (F). Burkeville, along FM 692, 31 Jul 2007, *DPL-8205* (F). **Orange Co.:** Vidor, near 455 Virginia Lane, 10 Oct 1993, *DPL-5035* (F). **Tyler Co.:** Dam-B, residence on CR 4136, off FM 92, N 30° 48.811', W 94° 12.600', 10 Jul 1995, *DPL-5498* (F). Temple-Inland Forest Lake Experimental Forest, *Quercus alba* test plot, 7 Aug 1995, *DPL-5573* (F). Big Thicket National Preserve, Beech Creek Unit, south boundary road, 14 Jul 2006, *DPL-7530* (F).

Boletus longicurvipes Snell & A.H. Smith. Found in mixed pine-hardwood forests, near baygall communities and in beech forests.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Jack Gore Baygall Unit, Arco Oil Field Road, 1 Aug 1982, *DPL-3233* (F); Saratoga, Lance Rosier Unit, Cotton Road, 20 Oct 1984, *DPL-3750* (F); Turkey Creek Unit, Kirby Nature Trail, 27 Oct 1984, *DPL-3767* (F). **Montgomery Co.:** Conroe, Kidd Road, Big Ron's Construction Office, N 30° 15.326', W 95° 25.481', 28 Jul 2007, *DPL-8176* (F). **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 26 Aug 2001, *DPL-6518* (F); 24 Jul 2007, *DPL-8151* (F). **Orange Co.:** Vidor, near 455 Virginia Lane, 30 Aug 1979, *DPL-1916* (F); 15 Aug 1982, *DPL-3317* (F).

FIGS. 1–4. 1. *Cortinarius aureifolius*. 2. *Phaeomarasmius cucurma*. 3. *Hygrocybe chamaeleon*. 4. *Tricholoma niveipes*. Scale bar = 10 mm.

Boletus morrisii Peck. Found in beech hammocks next to baygall communities.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Jack Gore Baygall Unit, Arco Oil Field Road, 5 Aug 1983, *DPL-3584* (F); 25 Sep 1983, *DPL-3617* (F).

Boletus rufomaculatus Both. Found in mixed pine-hardwood forests.

Voucher specimen: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 7 October 2004, *DPL-6929* (F).

Tylopilus eximius (Peck) Sing. Found in beech hammocks next to baygall communities.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Jack Gore Baygall Unit, Arco Oil Field Road, 25 Jun 1983, *DPL-3532* (F); 5 Aug 1983, *DPL-3585* (F); 25 Sep 1983, *DPL-3618* (F); 18 May 1984, *DPL-3651* (F); off FM 2937, 26 Jul 1985, *DPL-3878* (F). **Nacogdoches Co.:** Angelina National Forest, Stephen Austin Experimental Forest, 17 Sep 1994, *DPL-5338* (F).

Xanthoconium purpureum Snell & Dick. Found in bottomland hardwood forests.

Voucher specimens: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 1 Jul 1996, *DPL-5677* (TAES); 24 Jul 2007, *DPL-8154* (F).

Rhizopogon baxteri A.H. Smith. Known from Michigan and Mississippi.

Voucher specimen: **Hardin Co.:** Big Thicket National Preserve, Lance Rosier Unit, Saratoga, Teel Road, 15 Nov 2008, *DPL-8800* (F).

CANTHARELLALES

Craterellus odoratus (Schwein.) Fr. Found in mixed pine and hardwood forests.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Saratoga, Lance Rosier Unit, Teel Road, N 30° 15.629', W 94° 31.532', 13 Jun 2007, *DPL-7904* (F). **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630',18 Jul 2003, *DPL-6758* (F). **Polk Co.:** Big Thicket National Preserve, Big Sandy Unit, off CR 1071, 24 Jul 1976, *DPL-445* (F). **Tyler Co.:** Fred, residence on FM 1943, 8 May 1976, *DPL-23* (F).

HYMENOCHAETALES

Inonotus amplectans Murr. Found on living branch of *Asimina parviflora*.

Voucher specimens: **Newton Co.:** Lewis Chapel Community, Sand Ridge Cemetery, CR 4045, 30 Jul 2006, *DPL-7553* (F); 21 Jul 2007, *DPL-8134* (F).

POLYPORALES

Laetiporus persicinus (B. & C.) Gilbertson. Found at the base of tree/dead stump.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Lance Rosier Unit, Saratoga, Teel Rd, N 30° 15.629', W 94° 31.532', 17 Jun 2006, *DPL-7450* (TAES, PC); Turkey Creek Unit, Kirby Nature Trail, 22 Jul 2007, *DPL-8145* (F).

Pseudofavolus cucullatus (Mont.) Pat. A tropical species found on small branches and twigs.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Lance Rosier Unit, Saratoga, Teel Road, 15 Nov 2008, *DPL-8797* (F); Big Thicket National Preserve, Turkey Creek Unit, Kirby Nature Trail, 16 Jun 2007, *DPL-7999* (F); 22 Jul 2007, *DPL-8144* (F); Lumberton, Village Creek State Park, Nature trail, 23 Jun 2001, *DPL-6479* (LSU). **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 11 Jul 2000, *DPL-6342* (F).

RUSSULALES

PODOSCYPHACEAE

Cymatoderma caperatum (Berk. & Mont.) D.A. Reid. A tropical species found on wood.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Lance Rosier Unit, Saratoga, Teel Road, N 30° 15.629', W 94° 31.532', 13 Jun 2007, *DPL-7905* (F). **Harris Co.:** Pasadena, Armand Bayou Nature Center, 17 Nov 2007, *DPL-8325* (TAES).

RUSSULACEAE

Lactarius argillaceifolius Hesler & A.H. Smith. Found in mixed pine and hardwood forests.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Saratoga, Lance Rosier Unit, Teel Road, N 30° 15.629', W 94° 31.532', 11 Nov 2006, *DPL-7670* (TAES). **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 7 Sep 1996, *DPL-5709* (F); 29 Oct 1998, *DPL-6116* (F).

Lactarius atroviridis Peck. Found in mixed pine and hardwood forests.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Lance Rosier Unit, Cotton Road, near Saratoga, 15 Oct 1983, *DPL-3633* (F). **Nacogdoches Co.:** Angelina National Forest, Stephen F. Austin Experimental Forest, 17 Sep 1994, *DPL-5339* (F); 24 Sep 1994, *DPL-5340* (F). **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 17 Sep 1996, *DPL-5339* (F); 4 November 1998, *DPL-6121* (F); 11 Nov 2004, *DPL-7083* (TAES). **San Jacinto Co.:** Sam Houston National Forest, Big Creek Scenic Area, 10 Oct 1998, *DPL-6096* (F). **Tyler Co.:** Town Bluff, residence off FM 92, 29 May 1994, *DPL-5206* (F).

Lactarius caeruleitinctus Murr. Found in mixed pine and hardwoods forests.

Voucher specimen: **Newton Co.:** Bleakwood, 262 CR 3062, N 30° 42.509', W 93° 49.630', 30 August 1998, *DPL-6071* (F); 1 Jun 2004, *DPL-6874* (F).

Lactarius gerardii Peck. Found in hardwood forests.

Voucher specimens: **Hardin Co.:** Kountze, by Beaumont Creek, 12 Aug 1982, *DPL-3293* (F). **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 28 Jun 2003, *DPL-6727* (F); 17 Jun 1999, *DPL-6187* (F); 23 Oct 2004, *DPL-6983* (F). **Tyler Co.:** Big Thicket National Preserve, Neches River Corridor Unit, Round Lake, 13 Sep 2003, *DPL-6789* (F).

Lactarius imperceptus Beards. & Burl. Found in mixed pine and hardwoods.

Voucher specimens: **Angelina Co.:** Angelina National Forest, FR 313A, 2 Jan 2007, *DPL-7811* (F). **Hardin Co.:** Big Thicket National Preserve, Jack Gore Baygall Unit, near FM 2937, 28 Oct 1979, *DPL-2080* (F); Turkey Creek Unit, Kirby Nature Trail, 21 Dec 1982, *DPL-3405* (F); Big Thicket National Preserve, Saratoga, Lance Rosier Unit, Teel Road, N 30° 15.629', W 94° 31.532', 11 Nov 2006, *DPL-7672* (TAES). **Jasper Co.:** Buna, Temple-Inland Black Branch Hunting Club, road 2, off CR 701, off FM 1004, 5 Nov 1993, *DPL-5096* (F); 13 Nov 1993, *DPL-5116* (F). **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy 87, N 30° 42.509', W 93° 49.630', 1 Nov 1997, *DPL-5964* (F); 9 Nov 1997, *DPL-5969* (F); 18 Dec 2006, *DPL-7781* (F); Mayflower, Canyon Rim Nature Trail, 31.06.927 N, 93.43.752 W, 18 Dec 2007, *DPL-8415* (F). **Polk Co.:** Big Thicket National Preserve, Big Sandy Unit, Sunflower Road, 29 Nov 1985, *DPL-3932* (F). **Tyler Co.:** Big Thicket National Preserve, Turkey Creek Unit, off FM 1943, 15 Dec 1979, *DPL-2144* (F); Temple-Inland Forest Lake Experimental Forest, *Quercus nigra* test plot, 24 Nov 1995, *DPL-5594* (F); Big Thicket National Preserve, Canyonlands Unit, N 30° 06.927', W 93° 43.752', 20 Dec 2007, *Ovrebo 4720* (CSU) & *DPL-8444* (F).

Lactarius lignyotus var. **canadensis** A.H. Smith & Hesler. Found in sphagnum moss bog.

Voucher specimen: **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy. 87, N 30° 42.509', W 93° 49.630', 27 Sep 2003, *DPL-6824* (F).

Lactarius peckii Burl. Found in hardwood floodplain forests and with *Quercus alba*.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Jack Gore Baygall Unit, Timber Slough Road, 18 Jul 1981, *DPL-2735* (F). **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy. 87, N 30° 42.509', W 93° 49.630', 16 Jul 1995, *DPL-5518* (F); 19 Jun 1996, *DPL-5641* (F); 29 Oct 1998, *DPL-6115* (F). **Tyler Co.:** Big Thicket National Preserve, Turkey Creek Unit, off FM 1943, 9 Aug 1981, *DPL-2778* (F); Temple-Inland Forest Lake Experimental Forest, *Quercus nigra* test plot, 13 Jun 1993, *DPL-5011* (F); 22 Jun 1996, *DPL-5651* (F); 7 Jun 1997, *DPL-5788* (F); *Quercus alba* test plot, 30 May 1994, *DPL-5225* (F); 22 Jul 1995, *DPL-5550* (F); 7 Jun 1997, *DPL-5787* (F).

SEBACINALES

Sebacina concrescens (Schwein.) P. Roberts. Found in mixed pine and hardwood forests on a vine.

Voucher specimen: **Hardin Co.:** Big Thicket National Preserve, Saratoga, Lance Rosier Unit Teel Road, N 30° 15.629', W 94° 31.532', 19 Jul 2007, *DPL-8114* (F).

CORTICIALES

Punctularia strigosozonata (Schwein.) Talbot. Found on hardwood logs.

Voucher specimens: **Hardin Co.:** Big Thicket National Preserve, Turkey Creek Unit, Kirby Nature Trail, N 30° 27.738', W 94° 21.015', 14 Jun 2008, *DPL-8670* (F). **Newton Co.:** Bleakwood, 262 CR 3062 & State Hwy. 87, N 30° 42.509', W 93° 49.630', 13 Jan 2008, *DPL-8491* (F); Mayflower, Canyon Rim Nature Trail, N 31° 06.927', W 93° 43.752', 18 Dec 2007, *DPL-8427* (F).

ACKNOWLEDGMENTS

We thank the Big Thicket National Preserve for granting permission to collect in the Big Thicket. We are grateful to Scott Redhead, Ronald H. Petersen, and John McNeill for providing nomenclature assistance and advice; Roy E. Halling and The New York Botanical Garden for loaning the *Hygrophorus* type collections; Gastón Guzmán for confirming the identification of *Psilocybe caerulescens;* Sean Jones and Juan Luis Mata who assisted in various ways during the preparation of this manuscript; and Juan Luis Mata and Andrew Methven for reviewing the manuscript and providing helpful comments.

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BOOK REVIEW

Will Giles. 2007. **Encyclopedia of Exotic Pants for Temperate Climates.** (ISBN 978-0881927856, hbk.). Timber Press, 133 S.W. Second Ave., Suite 450, Portland, Oregon 97204-3527, U.S.A. (**Orders:** www.timberpress.com, 1-800-827-5622, 1-503-227-3070 fax). $49.95, 440 pp., 8 3/4" × 11 1/4".

The Victorian era and Victorians were captivated by the mysterious world of the exotic.

With their bold foliage, exuberant colors, and luscious scents, exotic plants ignited 19th century curiosity and thrilled Victorian senses. Fortunately for gardeners in the world's temperate regions, it's not necessary to live in the tropics nor own and operate a greenhouse to experience and enjoy growing exotic plants.

The *Encyclopedia of Exotic Plants for Temperate Climates* showcases a visually stunning array of exotic plants sure to delight gardeners who covet their dramatic effects and flamboyant beauty. Will Giles shows us how exotics can be persuaded to flourish in the unlikeliest places. He utilizes plants that are subtropical or tropical in appearance but that actually originate in cooler regions, as well as true tropicals and subtropicals that can flourish in temperate gardens.

More than 1500 species and cultivars are described in the encyclopedia, covering many plant groups, including aroids, bananas, gingers, bromeliads, cacti, yuccas, ferns, palms, and more. Detailed cultivation advice enables gardeners of all levels to make informed choices from the extensive plant list, and the information on geographic origins, microclimates, and recommended nurseries in the United Kingdom and North America enhances this comprehensive volume. Additional sources for further reading are interspersed throughout the text and collected in a bibliography. Electronic sources are supplied as well.

This book is richly illustrated with over 500 color photos. Most of the photos are larger than that required for identification. A good number are half-page size or larger. Their quality approaches an artistic level, one that has to be seen to be believed. Recommended for public libraries and research collections. It will appeal to all who enjoy some adventure in their gardening.

Will Giles, a lifelong exotic plants enthusiast, has created his own celebrated Exotic Garden in an unlikely location: England's east coast. Considered as the authority on growing exotic plants in temperate conditions, Will has appeared on a wide range of British television programs and contributes regularly to UK radio shows and magazines. Originally trained as an artist, he has worked as an illustrator for botanical books and is the author of *The New Exotic Garden* (2000).—*Gary L. Jennings, Librarian, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

TWENTY-EIGHT NEW THREE-LETTER FAMILY ACRONYMS FOR VASCULAR PLANTS (WITH COMPREHENSIVE LISTINGS ON-LINE)

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ABSTRACT

Three-letter acronyms are proposed for 28 newly recognized families of vascular plants. Complete listings alphabetically by family, and by acronym, are posted online at: http://www.conps.org/pdf/Plant%20Keys/ACROS.pdf.

RESUMEN

Se proponen acrónimos de tres letras para 28 familias nuevas de plantas vasculares. Listas completas por orden alfabético de familia, y de acrónimo, están disponibles online en: http://www.conps.org/pdf/Plant%20Keys/ACROS.pdf.

The use of three-letter acronyms (**TLA**) for plant families can expedite many routine aspects of curation (Weber 1982; Snow & Holton 2000; Brasher & Snow 2004a, b). TLA are used by some institutions in association with plant specimen labels, herbarium folders, filing systems, data bases, and plant checklists (Weber & Wittmann 1992; Snow 2009). If combined with a unique namespace, each TLA has the potential to be used as part of a globally unique identifier (GUID) for that family in bioinformatics applications.

Recent publications and online sources that synthesize the coverage of vascular plants at the family level for angiosperms (Stevens 2001; Heywood et al. 2007; Haston et al. 2007; Mabberley 2008) and ferns (Smith et al. 2006a, b) have begun to recognize families for which TLA previously were unavailable. This paper proposes 28 additional TLA for those families and integrates them into a comprehensive listing alphabetically by spelling of the family name and by three-letter acronym. The alphabetical lists (by family and by acronym) will also be available in pdf at: http://www.conps.org/pdf/Plant%20Keys/ACROS.pdf.

The following four acronyms are proposed for families of ferns: Cibotiaceae (CIB), Loxomataceae (LXM), Saccolomataceae (SCC), Tectariaceae (TCT).

The following 24 acronyms are proposed for angiosperms: Brownlowiaceae (BRW), Durionaceae (DUR), Calophyllaceae (CLP), Centroplacaceae (CTR), Eremolepidaceae (ERE), Eriospermaceae (ERS), Guamatelaceae (GUA), Haptanthaceae (HAP), Hostaceae (HOS), Johnsoniaceae (JHN), Leptaulaceae (LEP), Limeaceae (LME), Linderniaceae (LDR), Lophiocarpaceae (LOP), Nesogenaceae (NES), Pentapetaceae (PEN), Pteleocarpaceae (PTE), Samolaceae (SMO), Sparrmanniaceae (SPR), Stixaceae (STX), Syphostegiaceae (SYP), Talinaceae (TAL), Thomandersiaceae (THO), Viburnaceae (VIB). See Haston et al. (2007) for a recommended linear sequence for filing families based on updated versions of the APG II (2003) classification.

APPENDIX

The full alphabetical listings by family.

Abolbodaceae	ABB	Adoxaceae	ADX	Alangiaceae	ALG	Amaranthaceae	AMA
Acanthaceae	ACA	Aesculaceae	AES	Alismataceae	ALI	Amaryllidaceae	AML
Aceraceae	ACE	Aextoxicaceae	AEX	Alliaceae	ALL	Amborellaceae	ABL
Achariaceae	ACH	Agapanthaceae	AGP	Aloaceae	ALO	Ambrosiaceae	AMB
Achatocarpaceae	AHT	Agavaceae	AGA	Alseuosmiaceae	ASM	Amygdalaceae	AMY
Acoraceae	ACO	Agdestidaceae	AGD	Alsinaceae	ASN	Anacardiaceae	ANA
Actinidiaceae	ACT	Aitoniaceae	AIT	Alstroemeriaceae	ALS	Anarthriaceae	ANR
Actiniopteridaceae	ACP	Aizoaceae	AIZ	Altingiaceae	ALT	Ancistrocladaceae	ANC
Adiantaceae	ADI	Akaniaceae	AKA	Alzateaceae	ALZ	Androstachyaceae	AND

Anemarrhenaceae	ANE
Anemiaceae	ANM
Angiopteridaceae	ANG
Anisophylleaceae	ANS
Annonaceae	ANN
Anomochloaceae	AMO
Anthericaceae	ATH
Antoniaceae	ANT
Aphanopetalaceae	APN
Aphloiaceae	APL
Aphyllanthaceae	APH
Apiaceae	API
Apocynaceae	APO
Apodanthaceae	APD
Aponogetonaceae	APG
Apostasiaceae	APS
Aptandraceae	APT
Aquifoliaceae	AQF
Araceae	ARA
Araliaceae	ARL
Aralidiaceae	ARD
Araucariaceae	ARU
Arecaceae	ARE
Argophyllaceae	ARG
Aristolochiaceae	ARS
Asclepiadaceae	ASC
Asparagaceae	ASG
Asphodelaceae	ASP
Aspidiaceae	ASD
Aspleniaceae	ASL
Asteliaceae	ATL
Asteraceae	AST
Asteranthaceae	ASR
Asteropeiaceae	APE
Atherospermataceae	ATS
Athyriaceae	ATY
Aucubaceae	AUC
Austrobaileyaceae	AUS
Averrhoaceae	AVE
Avicenniaceae	AVI
Azollaceae	AZL
Balanitaceae	BLT
Balanopaceae	BLN
Balanophoraceae	BNP
Balsaminaceae	BLS
Barbeuiaceae	BBU
Barbeyaceae	BRB
Barclayaceae	BCL
Barringtoniaceae	BRR
Basellaceae	BAS
Bataceae	BAT
Baueraceae	BAU
Begoniaceae	BEG
Behniaceae	BEH
Berberidaceae	BER
Berberidopsidaceae	BBD
Betulaceae	BET
Biebersteiniaceae	BBS
Bignoniaceae	BIG
Bischofiaceae	BIS
Bixaceae	BIX
Blandfordiaceae	BLA
Blechnaceae	BLE
Blepharocaryaceae	BPC
Boerlagellaceae	BRL
Bombacaceae	BOM
Bonnetiaceae	BON
Boraginaceae	BOR
Boryaceae	BRY
Botrychiaceae	BTR
Brassicaceae	BRA
Bretschneideraceae	BRT
Brexiaceae	BRX
Bromeliaceae	BML
Brownlowiaceae	BRW
Brunelliaceae	BNL
Bruniaceae	BNI
Brunoniaceae	BNN
Buddlejaceae	BUD
Burmanniaceae	BMN
Burseraceae	BRS
Butomaceae	BUT
Buxaceae	BUX
Byblidaceae	BYB
Byttneriaceae	BYT
Cabombaceae	CAB
Cactaceae	CAC
Caesalpiniaceae	CSL
Calceolariaceae	CLI
Callitrichaceae	CLL
Calochortaceae	CCT
Calophyllaceae	CLP
Calycanthaceae	CAL
Calyceraceae	CLC
Campanulaceae	CAM
Campynemataceae	CPM
Canellaceae	CNL
Cannabaceae	CAN
Cannaceae	CNA
Canotiaceae	CNT
Capparaceae	CPP
Caprifoliaceae	CPR
Cardiopteridaceae	CRP
Caricaceae	CRC
Carlemanniaceae	CLM
Carpinaceae	CPN
Carpodetaceae	CAR
Cartonemataceae	CRT
Caryocaraceae	CCR
Caryophyllaceae	CRY
Cassythaceae	CSS
Casuarinaceae	CAS
Cecropiaceae	CEC
Celastraceae	CEL
Celtidaceae	CLT
Centrolepidaceae	CEN
Centroplacaceae	CTR
Cephalotaceae	CPH
Cephalotaxaceae	CTX
Ceratophyllaceae	CTP
Cercidiphyllaceae	CDP
Cheiropleuriaceae	CHI
Chenopodiaceae	CHN
Chloanthaceae	CLO
Chloranthaceae	CLR
Christenseniaceae	CHR
Chrysobalanaceae	CHB
Cibotiaceae	CIB
Cichoriaceae	CIC
Circaeasteraceae	CIR
Cistaceae	CIS
Cleomaceae	CMC
Clethraceae	CLE
Clusiaceae	CLU
Cneoraceae	CNR
Cobaeaceae	COB
Cochlospermaceae	CCH
Colchicaceae	CHC
Columelliaceae	COL
Combretaceae	CMB
Commelinaceae	CMM
Compositae	CMP
Connaraceae	CNN
Convallariaceae	CVL
Convolvulaceae	CNV
Coptaceae	COP
Cordiaceae	CRD
Coriariaceae	CRR
Coridaceae	COD
Cornaceae	COR
Corsiaceae	COS
Corylaceae	CRL
Corynocarpaceae	CNC
Costaceae	COT
Crassulaceae	CRS
Croomiaceae	CRM
Crossosomataceae	CRO
Cruciferae	CRU
Crypteroniaceae	CPT
Cryptogrammaceae	CRG
Ctenolophonaceae	CTL
Cucurbitaceae	CUC
Culcitaceae	CUL
Cunoniaceae	CUN
Cupressaceae	CUP
Curtisiaceae	CUR
Cuscutaceae	CUS
Cyanastraceae	CYN
Cyatheaceae	CTH
Cycadaceae	CCD
Cyclanthaceae	CYC
Cyclocheilaceae	CCC
Cymodoceaceae	CYM
Cynomoriaceae	CNM
Cyperaceae	CYP
Cypripediaceae	CPD
Cyrillaceae	CYR
Cytinaceae	CYT
Danaeaceae	DAN
Daphniphyllaceae	DPH
Dasypogonaceae	DAS
Datiscaceae	DAT
Davalliaceae	DAV
Davidiaceae	DVD
Davidsoniaceae	DVS
Degeneriaceae	DEG
Dennstaedtiaceae	DST
Desfontainiaceae	DSF
Dialypetalanthaceae	DLP
Diapensiaceae	DIA
Dichapetalaceae	DCH
Dichondraceae	DCO
Dicksoniaceae	DCK
Diclidantheraceae	DCL
Dicrastylidaceae	DCR
Didiereaceae	DID
Didymelaceae	DDM
Diegodendraceae	DGD
Diervillaceae	DIE
Dilleniaceae	DLL
Dioncophyllaceae	DON
Dioscoreaceae	DSC
Dipentodontaceae	DPN
Dipsacaceae	DPS
Dipteridaceae	DPT
Dipterocarpaceae	DPC
Dirachmaceae	DCM
Dodonaeaceae	DOD
Donatiaceae	DNT
Doryanthaceae	DOR
Dracaenaceae	DRC
Droseraceae	DRS
Drosophyllaceae	DRO
Dryopteridaceae	DRY
Duckeodendraceae	DUK
Dulongiaceae	DUL
Durionaceae	DUR
Ebenaceae	EBN
Ecdeiocoleaceae	ECD
Ehretiaceae	EHR
Elaeagnaceae	ELE
Elaeocarpaceae	ELC
Elaphoglossaceae	ELP
Elatinaceae	ELT
Elodeaceae	ELO
Emblingiaceae	EMB
Empetraceae	EMP
Epacridaceae	EPC
Ephedraceae	EPH
Equisetaceae	EQU
Eremolepidaceae	ERE
Eremosynaceae	ERM

Ericaceae	ERI	Hanguanaceae	HNG	Juglandaceae	JUG	Mackinlayaceae	MCK
Eriocaulaceae	ERO	Haptanthaceae	HAP	Julianiaceae	JUL	Maesaceae	MAE
Eriospermaceae	ERS	Hectorellaceae	HCT	Juncaceae	JUN	Magnoliaceae	MAG
Erythropalaceae	ERP	Heliconiaceae	HLC	Juncaginaceae	JCG	Malaceae	MAL
Erythroxylaceae	ERX	Heliotropiaceae	HLT	Kaliphoraceae	KLP	Malesherbiaceae	MLH
Escalloniaceae	ESC	Helleboraceae	HEL	Kaulfussiaceae	KLF	Malpighiaceae	MLP
Eucommiaceae	ECM	Helminthostachyaceae	HLM	Kingdoniaceae	KGD	Malvaceae	MLV
Eucryphiaceae	ECR	Helwingiaceae	HLW	Kirkiaceae	KRK	Marantaceae	MRN
Euphorbiaceae	EUP	Hemerocallidaceae	HMR	Koeberliniaceae	KBL	Marattiaceae	MTT
Euphroniaceae	EPR	Hemionitidaceae	HEM	Krameriaceae	KRM	Marcgraviaceae	MRC
Eupomatiaceae	EPM	Henriqueziaceae	HRQ	Labiatae	LAB	Marsileaceae	MSL
Eupteleaceae	EPT	Hernandiaceae	HRN	Lacistemataceae	LCS	Martyniaceae	MAR
Euryalaceae	EUR	Herreriaceae	HRR	Lactoridaceae	LCT	Mastixiaceae	MSX
Fabaceae	FAB	Hesperocallidaceae	HSP	Lamiaceae	LAM	Matoniaceae	MAT
Fagaceae	FAG	Heteropyxidaceae	HTP	Lanariaceae	LAN	Mayacaceae	MAY
Ficoidaceae	FIC	Himantandraceae	HMT	Lardizabalaceae	LAR	Medusagynaceae	MDG
Flacourtiaceae	FLC	Hippocastanaceae	HCS	Lauraceae	LAU	Medusandraceae	MDA
Flagellariaceae	FLG	Hippocrateaceae	HPC	Laxmanniaceae	LAX	Melanophyllaceae	MLA
Flindersiaceae	FLN	Hippuridaceae	HPU	Lecythidaceae	LCY	Melanthiaceae	MLN
Foetidiaceae	FOE	Hoplestigmataceae	HPT	Ledocarpaceae	LDC	Melastomataceae	MLS
Fouquieriaceae	FOQ	Hostaceae	HOS	Leeaceae	LEE	Meliaceae	MEL
Francoaceae	FCO	Huaceae	HUA	Leguminosae	LEG	Melianthaceae	MTH
Frankeniaceae	FNK	Hugoniaceae	HUG	Leitneriaceae	LTN	Meliosmaceae	MLO
Fumariaceae	FUM	Humbertiaceae	HMB	Lemnaceae	LMN	Memecylaceae	MMC
Garryaceae	GAR	Humiriaceae	HOU	Lennoaceae	LNN	Mendonciaceae	MND
Geissolomataceae	GSL	Huperziaceae	HUP	Lentibulariaceae	LNT	Menispermaceae	MNS
Gelsemiaceae	GEL	Hyacinthaceae	HYA	Leonticaceae	LEO	Menthaceae	MEN
Gentianaceae	GEN	Hydatellaceae	HYT	Lepidobotryaceae	LPB	Menyanthaceae	MNY
Geosiridaceae	GEO	Hydnoraceae	HDN	Leptaulaceae	LEP	Mesembryanthemaceae	MSM
Geraniaceae	GER	Hydrangeaceae	HDR	Lepuropetalaceae	LPR	Mespilaceae	MSP
Gesneriaceae	GSN	Hydrastidaceae	HDS	Lilaeaceae	LLA	Metaxyaceae	MTX
Ginkgoaceae	GNK	Hydrocaryaceae	HCY	Liliaceae	LIL	Metteniusaceae	MET
Gisekiaceae	GIS	Hydrocharitaceae	HDC	Limeaceae	LME	Mimosaceae	MIM
Glaucidiaceae	GCD	Hydrocotylaceae	HCO	Limnanthaceae	LIM	Misodendraceae	MIS
Gleicheniaceae	GLC	Hydroleaceae	HDL	Limnocharitaceae	LMC	Mitrastemonaceae	MTR
Globulariaceae	GLB	Hydrophyllaceae	HYD	Limoniaceae	LMO	Molluginaceae	MOL
Gnetaceae	GNE	Hydrostachyaceae	HST	Linaceae	LIN	Monachosoraceae	MCS
Goetzeaceae	GTZ	Hymenophyllaceae	HMP	Linderniaceae	LDR	Monimiaceae	MNM
Gomortegaceae	GOM	Hymenophyllopsidaceae	HPS	Lindsaeaceae	LND	Monotropaceae	MNT
Gonystylaceae	GNS	Hypecoaceae	HYC	Linnaeaceae	LNA	Montiniaceae	MTN
Goodeniaceae	GOD	Hypericaceae	HYP	Lissocarpaceae	LSS	Moraceae	MOR
Goupiaceae	GOU	Hypolepidaceae	HPL	Loasaceae	LOA	Morinaceae	MNA
Gramineae	GRM	Hypoxidaceae	HPX	Lobeliaceae	LOB	Moringaceae	MRG
Grammitidaceae	GMM	Hypseocharitaceae	HSC	Loganiaceae	LOG	Muntingiaceae	MUN
Greyiaceae	GRY	Icacinaceae	ICC	Lophiocarpaceae	LOP	Musaceae	MUS
Griseliniaceae	GRI	Ilicaceae	ILI	Lomariopsidaceae	LOM	Myodocarpaceae	MYD
Grossulariaceae	GRS	Illecebraceae	ICB	Lophiraceae	LPI	Myoporaceae	MYO
Grubbiaceae	GRB	Illiciaceae	ILC	Lophopyxidaceae	LPX	Myricaceae	MYR
Guamatelaceae	GUA	Iridaceae	IRI	Lophosoriaceae	LPH	Myriophyllaceae	MPH
Gunneraceae	GNN	Irvingiaceae	IRV	Loranthaceae	LOR	Myristicaceae	MYS
Guttiferae	GUT	Isoetaceae	ISO	Lowiaceae	LOW	Myrothamnaceae	MTM
Gymnogrammitidaceae	GGR	Iteaceae	ITE	Loxogrammaceae	LOX	Myrsinaceae	MRS
Gyrostemonaceae	GYR	Ixerbaceae	IXR	Loxomataceae	LXM	Myrtaceae	MRT
Haemodoraceae	HAE	Ixioliriaceae	IXI	Loxosomataceae	LXS	Myzodendraceae	MYZ
Halesiaceae	HLS	Ixonanthaceae	IXO	Luzuriagaceae	LUZ	Najadaceae	NAJ
Halophytaceae	HPH	Japonoliriaceae	JAP	Lycopodiaceae	LYC	Nandinaceae	NAN
Haloragaceae	HAL	Johnsoniaceae	JHN	Lygodiaceae	LYG	Napoleonaeaceae	NAP
Hamamelidaceae	HAM	Joinvilleaceae	JNV	Lythraceae	LYT	Nartheciaceae	NAR

Naucleaceae	NAU	Petrosaviaceae	PSV	Rafflesiaceae	RAF	Smilacaceae	SML
Negripteridaceae	NEG	Phellinaceae	PLN	Ranunculaceae	RAN	Solanaceae	SOL
Nelumbonaceae	NEL	Philadelphaceae	PHD	Rapateaceae	RPT	Sonneratiaceae	SNN
Nepenthaceae	NEP	Philesiaceae	PLS	Resedaceae	RSD	Sparganiaceae	SPG
Nephrolepidaceae	NPH	Philydraceae	PHL	Restionaceae	RST	Sparrmanniaceae	SPR
Nesogenaceae	NES	Phormiaceae	PHO	Retziaceae	RTZ	Sphaerosepalaceae	SPS
Neumanniaceae	NMN	Phrymaceae	PHR	Rhabdodendraceae	RHB	Sphenocleaceae	SPC
Neuradaceae	NRD	Phyllanthaceae	PLL	Rhamnaceae	RHM	Sphenostemonaceae	SPH
Nitrariaceae	NIT	Phyllocladaceae	PCL	Rhipogonaceae	RIP	Spigeliaceae	SGL
Nolanaceae	NOL	Phylionomaceae	PHN	Rhizophoraceae	RHZ	Spiraeaceae	SPI
Nolinaceae	NLN	Physenaceae	PHY	Rhodoleiaceae	RHD	Stachyuraceae	STC
Nothofagaceae	NTF	Phytolaccaceae	PHT	Rhoipteleaceae	RHP	Stackhousiaceae	STK
Nyctaginaceae	NYC	Picramniaceae	PIC	Rhopalocarpaceae	RPL	Stangeriaceae	SNG
Nymphaeaceae	NYM	Picrodendraceae	PCR	Rhynchocalycaceae	RNC	Staphyleaceae	STP
Nypaceae	NYP	Pinaceae	PIN	Roridulaceae	RRD	Stegnospermataceae	STG
Nyssaceae	NYS	Piperaceae	PIP	Rosaceae	ROS	Stemonaceae	STM
Ochnaceae	OCH	Pistaciaceae	PIS	Rousseaceae	ROU	Stemonuraceae	STO
Octoknemaceae	OCT	Pittosporaceae	PIT	Rubiaceae	RUB	Stenomeridaceae	STN
Olacaceae	OLC	Plagiogyriaceae	PGY	Ruppiaceae	RUP	Sterculiaceae	STR
Oleaceae	OLE	Plagiopteraceae	PGP	Ruscaceae	RUS	Stilaginaceae	SGN
Oleandraceae	OLN	Plantaginaceae	PTG	Rutaceae	RUT	Stilbaceae	STL
Oliniaceae	OLI	Platanaceae	PLT	Sabiaceae	SAB	Stixaceae	STX
Onagraceae	ONA	Platyzomataceae	PTZ	Saccolomataceae	SCC	Strasburgeriaceae	STS
Oncothecaceae	ONC	Plocospermataceae	PLO	Salicaceae	SAL	Strelitziaceae	SRZ
Onocleaceae	ONO	Plumbaginaceae	PLB	Salvadoraceae	SLV	Streptochaetaceae	SEP
Ophioglossaceae	OPH	Poaceae	POA	Salviniaceae	SVN	Stromatopteridaceae	STT
Opiliaceae	OPI	Podoaceae	POD	Sambucaceae	SMB	Strychnaceae	SRY
Orchidaceae	ORC	Podocarpaceae	PDC	Samolaceae	SMO	Stylidiaceae	SYD
Orobanchaceae	ORO	Podophyllaceae	PDP	Samydaceae	SAM	Stylobasiaceae	SLB
Osmundaceae	OSM	Podostemaceae	PDS	Saniculaceae	SNC	Stylocerataceae	SLC
Oxalidaceae	OXL	Polemoniaceae	PLM	Santalaceae	SAN	Styracaceae	STY
Paeoniaceae	PAE	Polygalaceae	PGL	Sapindaceae	SAP	Surianaceae	SUR
Palmae	PAL	Polygonaceae	PLG	Sapotaceae	SPT	Symphoremataceae	SRM
Pandaceae	PDA	Polyosmaceae	POL	Sarcobataceae	SRB	Symplocaceae	SYM
Pandanaceae	PND	Polypodiaceae	PLP	Sarcolaenaceae	SRC	Syphostegiaceae	SYP
Papaveraceae	PAP	Pontederiaceae	PON	Sarcospermataceae	SSP	Taccaceae	TAC
Papilionaceae	PPL	Populaceae	POP	Sargentodoxaceae	SRG	Taenitidaceae	TAE
Paracryphiaceae	PCP	Portulacaceae	POR	Sarraceniaceae	SAR	Talinaceae	TAL
Parkeriaceae	PRK	Posidoniaceae	POS	Saurauiaceae	SRA	Tamaricaceae	TAM
Parnassiaceae	PAR	Potaliaceae	PTL	Saururaceae	SRR	Tapisciaceae	TAP
Passifloraceae	PAS	Potamogetonaceae	POT	Saxifragaceae	SAX	Taxaceae	TAX
Paulowniaceae	PAU	Pottingeriaceae	PTT	Scheuchzeriaceae	SZR	Taxodiaceae	TXO
Pedaliaceae	PED	Primulaceae	PRM	Schisandraceae	SCS	Tecophilaeaceae	TEC
Peganaceae	PEG	Prioniaceae	PRI	Schizaeaceae	SCZ	Tectariaceae	TCT
Pellicieraceae	PEL	Proteaceae	PRT	Schlegeliaceae	SCH	Tepuianthaceae	TEP
Penaeaceae	PNA	Psilotaceae	PSL	Schoepfiaceae	SPF	Ternstroemiaceae	TRN
Pennantiaceae	PNN	Psiloxylaceae	PSX	Sciadopityaceae	SCI	Tetracarpaeaceae	TCA
Pentadiplandraceae	PNT	Ptaeroxylaceae	PTX	Scrophulariaceae	SCR	Tetracentraceae	TTR
Pentapetaceae	PEN	Pteleocarpaceae	PTE	Scyphostegiaceae	SST	Tetrachondraceae	TTC
Pentaphragmataceae	PTP	Pteridaceae	PTR	Scytopetalaceae	SCT	Tetradiclidaceae	TDC
Pentaphylacaceae	PHC	Pteridophyllaceae	PPH	Selaginellaceae	SEL	Tetragoniaceae	TTG
Penthoraceae	PTH	Pterostemonaceae	PTS	Setchellanthaceae	SET	Tetramelaceae	TTM
Peperomiaceae	PEP	Punicaceae	PUN	Simaroubaceae	SMR	Tetrameristaceae	TMR
Peraceae	PER	Putranjivaceae	PUT	Simmondsiaceae	SMM	Thalictraceae	THA
Peridiscaceae	PRD	Pyrolaceae	PYR	Sinopteridaceae	SIN	Theaceae	TEA
Periplocaceae	PRP	Quiinaceae	QII	Siparunaceae	SIP	Theligonaceae	THG
Petermanniaceae	PTM	Quillajaceae	QLJ	Siphonodontaceae	SPD	Thelypteridaceae	THL
Petiveriaceae	PTV	Quintiniaceae	QNT	Sladeniaceae	SLD	Themidaceae	THE

Theophrastaceae	TEO	Tremandraceae	TMD	Umbelliferae	UMB	Wellstediaceae	WLS
Thismiaceae	THS	Tribelaceae	TRB	Urticaceae	URT	Welwitschiaceae	WLW
Thomandersiaceae	THO	Trichomanaceae	TCM	Uvulariaceae	UVU	Winteraceae	WIN
Thunbergiaceae	THN	Trichopodaceae	TCH	Vacciniaceae	VAC	Woodsiaceae	WDS
Thurniaceae	THU	Trigoniaceae	TRG	Vahliaceae	VHL	Xanthophyllaceae	XPH
Thymelaeaceae	THY	Trilliaceae	TRL	Valerianaceae	VAL	Xanthorrhoeaceae	XAN
Thyrsopteridaceae	THR	Trimeniaceae	TRM	Velloziaceae	VLL	Xeronemataceae	XER
Ticodendraceae	TIC	Triplostegiaceae	TPS	Verbenaceae	VRB	Xyridaceae	XYR
Tiliaceae	TIL	Tristichaceae	TRS	Violaceae	VIO	Zamiaceae	ZAM
Tmesipteridaceae	TMS	Triuridaceae	TRI	Virburnaceae	VIB	Zannichelliaceae	ZAN
Tofieldiaceae	TOF	Trochodendraceae	TRC	Viscaceae	VIS	Zingiberaceae	ZIN
Torricelliaceae	TOR	Tropaeolaceae	TRP	Vitaceae	VIT	Zosteraceae	ZOS
Tovariaceae	TOV	Turneraceae	TNR	Vittariaceae	VTT	Zygophyllaceae	ZYG
Trapaceae	TRA	Typhaceae	TYP	Vivianiaceae	VIV		
Trapellaceae	TPL	Ulmaceae	ULM	Vochysiaceae	VOC		

ACKNOWLEDGMENTS

My thanks to K. Richards (Landcare Research, New Zealand), E. Haston (E) and W. Judd (FLAS) for their comments, and to Al Schneider and the Colorado Native Plant Society for agreeing to post the complete listings online.

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BOOK REVIEW

Janet Chui and Jason Lundberg. 2008. **A Field Guide to Surreal Botany.** (ISBN 978-9810810177, pbk.). Two Cranes Press, Singapore Post Centre, P.O. Box 034, Singapore 914002. (**Orders:** www.twocranespress.com). $12.00, 70 pp., 5 1/2" × 8".

A Field Guide to Surreal Botany is an anthology of fictional plant species that exist beyond the realm of the real. Another work in the same genre is *Parallel Botany*, by Leo Lionni. This small book is a bit of lunacy sure to appeal to slightly twisted plant lovers and botanists everywhere.

As they say, presentation is everything. This appears to be an old-fashioned botanical treatise with its delicate illustrations, Latin names, notes on ecology and life cycle, and seemingly aged paper. Great care has been put into making the entries read as real and authentic, but the sly hints and literary winks let the readers know they are in on some way-cool joke with the writers. It is an example of what can be done when you lavish care and attention on a literary project. It literally oozes quality. This is a small press title that exceeded my expectations and is irresistible on every level.

It is arranged geographically by regions of the world and fully illustrated by Janet Chui. It is hard to choose a favorite from among the many species. Amongst my favorites are the Forget-me-bastard which merely causes itching, stinging, and rash in defense of the main caregiver of the garden in which they grow; the Time Cactus that can trick the unwary researcher or amateur botanist into a quite deadly trance (sending their nutrients back along a wormhole to a previous time of scarcity); and the Kvetching Aspen, which is the only known tree with a mating cry.

Janet Chui and Jason Lundberg met at the 2002 Clarion Writers Workshop in Michigan. They formed Two Cranes Press, an independent publisher, in 2003, and moved from Raleigh, North Carolina, to Singapore where it is now based. Two Cranes was set up to publish speculative fiction and has published three other works.—*Gary L. Jennings, Librarian, Botanical Research Institute of Texas, Fort Worth, Texas 76102-4025, U.S.A.*

CHROMOSOME NUMBERS OF MISCELLANEOUS ANGIOSPERM TAXA

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ABSTRACT

Chromosome counts are reported for 68 individuals in 64 taxa (including one interspecific hybrid) in 36 genera of 15 families. Of these, 11 taxa are counted for the first time.

RESUMEN

Se recontaron los números cromosómicos de 68 individuos en 64 taxones (incluyendo un híbrido interspecífico) pertenecientes a 36 géneros de 15 familias. De estos, 11 taxones se han contado por primera vez aquí.

METHODS

Meiotic counts (*n*) were obtained from microsporogenesis in flower buds according to methods of Pinkava et al. (1998); mitotic counts (2*n*) were obtained from root tips according to Cota et al. (1994).

RESULTS

First counts are reported for: *Agave felgeri, A. margaritae, A. mckelveyana* (Agavaceae); *Cylindropuntia anteojoensis* × *C. leptocaulis, Escontria chiotilla, Stenocactus multicostatus, Stenocereus beneckei* (Cactaceae); *Mosiera ehrenbergii* (Myrtaceae), *Eriogonum ripleyi* (Polygonaceae), *Nemeranthus validulus* (Portulacaceae) and *Ivesia multifoliolata* (Rosaceae). A new count was made for *Prunus virginiana* var. *demissa* (Rosaceae). Other counts are listed below (Table 1).

Table 1. Vouchered chromosome number reports of miscellaneous angiosperms. Counts were determined by the collector of the numbered specimen unless in brackets with initials of an author of this paper. Vouchers are deposited in herbaria whose acronyms (Holmgren, P. K. et al. 1990) appear in parentheses. Asterisks (*) denote first counts; (**) denote a new chromosome number for a taxon.

Taxon	Chromosome number	Locality, notes
	DICOTYLEDONAE	
Apocynaceae		
Amsonia tomentosa Torr. & Frémont var. *tomentosa*	*n* = 11	USA, Arizona, Mohave Co.: NNW of Alamo Lake, jctn. Signal and Alamo Rds., *Parfitt 4181B* & *Christy* (ASU).
Asteraceae / Compositae		
Coreocarpus parthenioides Benth. var. *parthenioides*	*n* = 12	MEX, Baja California: 5.3 km S of town of Bahia de Los Angeles, *Rebman 957* & *Marsh* (ASU)

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J. Bot. Res. Inst. Texas 3(1): 279 – 283. 2009

TABLE 1. (continued)

Taxon	Chromosome number	Locality, notes
	DICOTYLEDONAE	
Lasthenia coronaria (Nutt.) Ornduff	*n* = 4	MEX, Baja California: 4.8 km S of Punta Baja W of El Rosario, *Rebman 927* & *Marsh* (ASU).
Perityle crassifolia Brandegee var. *robusta* (Rydb.) Everly	*n* = 19	MEX, Baja California Sur: 3 km S of San Gregorio, *Baker 8767* & *Johnson* (ASU).
Perityle lobata (Rydb.) I.M. Johnst.	*n* = 17	MEX, Baja California Sur: 0.8 km E of San José, Comondú, *Baker 8748* & *Johnson* (ASU).
Senecio californicus DC.	*n* = 20	MEX, Baja California: 4.8 km S of Punta Baja W of El Rosario, *Rebman 930* & *Marsh* (ASU).
Stephanomeria schottii A. Gray	*n* = 8	USA, Arizona, Yuma Co.: Mohawk Dunes, T9S R15W S2, *Salywon 557* & *Shohet* (ARIZ, ASU, DES, SD).
Viguiera laciniata A. Gray	*n* = 18	MEX, Baja California: N of El Junco, between Ensenada and Tijuana, *Rebman 2156* & *Hirales* (ASU).
Brassicaceae / Cruciferae		
Cakile maritima Scopoli	*n* = 9	MEX, Baja California: Punta Morro, N of Ensenada, *Rebman 2153* (ASU).
Hesperidanthus linearifolius (A. Gray) Rydb.	*n* = 11	USA, Arizona, Coconino Co.: 32 km N of Flagstaff on Hwy 180, *Salywon 256* (ASU).
Cactaceae		
Cleistocactus cf. *baumannii* Lem.	*n* = 11	Origin unknown; cultiv. at Univ. of Tennessee and Arizona State Univ., *Christy s.n.* (ASU).
**Consolea corallicola* Small	2*n* = 66	USA, Florida, Monroe Co.: Torchwood Hammock, Little Torch Key, Bob Ehrig, TNC. Cultiv. Fairchild Tropical Gardens (FTG 90-04), Miami, and Arizona State Univ., Tempe; recollected 14 June 1990 by Pinkava (ASU). [JHC] Previously published (Austin et al. 1998) without details.
Consolea rubescens (Salm-Dyck ex DC.) Lem.	2*n* = 132	West Indies, Guadeloupe: Pointe de la Grand Vigie, Grand Terre (R. Moyround); cultiv. in GeminiGardens, Manalapan, Florida, and at ASU. Greenhouse, Tempe, *Pinkava s.n.* (ASU). [JHC]
**Cylindropuntia anteojoensis* (Pinkava) E.F. Anderson × *C. leptocaulis* (DC.) F.M. Kunth	*n* = 22	MEX, Coahuila: S side of Sierra de la Fragua, near Cuatro Cienegas, *Salywon 153* & *Tiller* (ASU).
Cylindropuntia imbricata (Haw.) F.M. Knuth var. *imbricata*	*n* = 11	MEX, S.L.P.: Municipio Santa Catarina, *Puente 1258* (ASU).
Echinocereus pensilis (K. Brandegee) Purpus [*Morangaya pensilis* (K. Brandegee) C.D. Rowley]	*n* = 11	Origin unknown; cultiv. in Scottsdale, Arizona, *Zimmerman 2665* (ASU). [BP]
Echinocereus scheeri (Salm-Dyck) Scheer subsp. *gentryi* (Clover) N.P. Taylor	*n* = 11	Origin unknown; cultiv. in Tucson, Arizona, *Zimmerman 2774* (ASU).
Echinocereus viridiflorus Engelm. var. *viridiflorus*	*n* = 11	USA, Colorado, Lincoln Co.: Punkin Center, Highway 71, *Salywon 110a* (ASU).
Echinomastus intertextus (Engelm.) Britton & Rose var. *intertextus*	*n* = 11	USA, Arizona, Pima Co.: Cienega Creek, *Salywon 115* & *Tiller*.
Echinomastus johnsonii (Engelm.) E.M. Baxter	*n* = 11	USA, Arizona, Mohave Co.: vicinity of Lake Mead, purple flowers, *Chamberland 58* (ASU). [?BP]
Eriosyce subgibbosa (Haw.) Katt. subsp. *clavata* (Söhrens ex Schum.) Katt. var. *nigrihorrida* (Backeb.) Katt.	*n* = 11	Chile, Coqimbo, Ritter 218, [Dr. J. Barrow's collection No. 36] Atlanta Bot. Gard., then cultiv. in Desert Bot. Gard., Arizona (DBG 1992-0203-01-01), recollected by E.F. Anderson (DES). [BP]

Table 1. (continued)

Taxon	Chromosome number	Locality, notes
	DICOTYLEDONAE	
**Escontria chiotilla* (F.A.C. Weber) Rose	$n = 11$	Origin unknown; cultiv. at Desert Bot. Gard., Arizona (Bed D, DBG #1950-2731-01-01), *Chamberland s.n.* (ASU). [DP, JR]
Hatiora salicornioides (Haw.) Britton & Rose	$n = 11$	Origin unknown; cultiv. in ASU greenhouse, Tempe, *Rebman s.n.* (ASU, SD).
Opuntia aciculata Griffiths	$n = 22$	Origin unknown; in Desert Bot.Gard., Arizona (Bed 57W, DBG 76-73), *Hodgson 3644* (ASU photo, DES). [DP]
Opuntia elatior P. Miller	$n = 44$	Origin from International Succulent Institute, possibly in Colombia; cultiv. at Desert Bot. Gard., Arizona (DBG 168-9268-01-01) recollected by *J. Ward s.n.* (DES, 2 sheets). [JR; meiosis irregular]
Opuntia humifusa (Raf.) Raf.	$2n = 22$	USA, Florida: pineland remnant (from Montgomery Foundation). Cultiv. in Fairchild Tropical Garden, Florida (FTG 90-107) and in ASU Greenhouse, Arizona, *Pinkava s.n.* (originally labeled as var. *austrina* (Small) Dress [JHC].
Opuntia humifusa (Raf.) Raf.	$n = 11$	USA, Georgia, Bullock Co.: 3.2 km N of Lotts Creek Bridge, 9.7 km S of Statesboro, *Christy 2741b* (ASU, DES, SD). Richmond Co.: Augusta, 3.2 km SW of jctn. I-20 & I-520, *Christy 2748-A1* (ASU), *-A12* (ASU, NY, US). South Carolina, Lexington Co.: 48 km W of Columbia, *Christy 2745B* (ASU, NY, US).
Opuntia megarhiza Rose [*O. pachyrrhiza* Gómez-Hin. & Bárcenas]	$n = 11$	MEX, S.L.P.: Mpio. Zaragoza, 1 km N of Valley de Los Fantasmas, *Puente 601* (ASU, two sheets).
Opuntia salmiana Parm. ex Pfeiff.	$n =$ ca. 22 (irreg. tetrads)	Origin unknown; cultiv. in Scottsdale, Arizona, *Zimmerman s.n.* (ASU).
Opuntia stricta (Haw.) Haw.	$n = 22$	Origin unknown; cultiv. (as var. *dillenii*) in Scottsdale, Arizona, *Zimmerman 2667* (ASU). [BP]
Stenocactus crispatus (DC.) A. Berger ex A.W. Hill [*Echinofossulocactus crispatus* DC.) Lawrence]	$n = 11$	MEX, S.L.P.,13 km S of Huizache Junction, Rod *McGill s.n.*; then cultiv., Desert Bot. Gard., Arizona (DBG 1962-7221-01-01). Recollected by J. Ward (DES). [BP]
Stenocactus multicostatus (Hildeman ex K. Schum.) A. Berger [*Echinofossulocactus multicostatus* (K. Schum.) Britton & Rose]	$n = 11$	Origin unknown. Cultiv. in Mesa, Arizona, *Puente 538* (ASU, two sheets, one box). [RP & JR]
**Stenocereus beneckei* (Ehrenb.) A. Berger & F. Buxbaum	$n = 11$	Origin unknown; cultiv. in Desert Bot. Gard. Arizona (Webster Patio near Library), *Parfitt s.n.* (ASU).
Stenocereus pruinosus (Otto) F. Buxbaum	$n = 11$	MEX, Colima: Manzanillo, C. Meig & F. G. Hermann, in 1955. Cultiv. in Desert Bot. Gard., Arizona (DBG 5143-01-01), *Chamberland s.n.* (ASU, DES).
Stenocereus stellatus (Pfeiff.) Riccobono	$n = 11$	MEX, PUEBLA: near Tehuacan, *Lindsay s.n.*; cultiv., Desert Bot. Gard., Arizona (DBG 139-0628-0104); recollected by J. Ward. (ASU, DES).
Crassulaceae		
Dudleya arizonica Rose	$n = 17$	MEX, Baja California: 3.2 km SE of San Matias Pass, San Pedro Mártir, *Baker 3716* (ASU).
Dudleya ingens Rose	$n = 34$	MEX, Baja California: 3.2 km W of Camalu on Rte. 1, *Gallagher 82-40* (ASU). [MB]
Fabaceae / Leguminosae		
Astragalus nutriosensis Sanderson	$n = 11$	USA, Arizona, Apache Co.: SE of Eager, Picnic Hill just W of Rte. 666, *Baker 11431.2* & *Wright* (ASU).

Table 1. (continued)

Taxon	Chromosome number	Locality, notes
	DICOTYLEDONAE	
Astragalus oophorus S. Watson var. *caulescens* (M.E. Jones) M.E. Jones	*n* = 11	USA, Arizona, Coconino Co.: 5 km N of Jacob Lake, *Baker 4387* & *Trushell* (ASU).
Astragalus trichopodus (Nutt.) A. Gray var. *lonchus* (M.E. Jones) Barneby	*n* = 15	MEX, Baja California; 2 km E of Rosalallita, Santo Domingo Wash, *Baker 8701* & *Johnson*, Hwy 1, 86 km S of San Quintin, *Rebman 1646* & *Delgadillo* (ASU).
Astragalus troglodytus S. Watson	*n* = 11	USA, Arizona, Yavapai Co.: NW of Prescott, 0.8 km SW of Lone Pine Tank, *Baker 10652* (ASU).
Lupinus latifolius Agardh subsp. *leucanthus* (Rydb.) Kenny & Dunn	*n* = 24	USA, Arizona, Yavapai Co.: NW of Prescott, 1.4 km WNW of Stinson Mtn., *Baker 11023.1* & *Wright* (ASU).
Psoralidium tenuiflora (Pursh) Rydb.	*n* = 11	USA, Arizona, Yavapai Co.: NW of Prescott, 3.7 km SW of Connell Mtn. summit, *Baker 10843* (YCH).
Lamiaceae / Labiatae		
Salvia dorrii (Kellogg) Abrams subsp. *mearnsii* (Britton) McClintock	*n* = 15	USA, Arizona, Yavapai Co.: 4 km WSW of confluence of Hell Canyon and Verde River, 1.5 km NW of Verde Ranch Headquarters, *Baker 15697* (ARIZ, ASC, ASU, DES).
Loasaceae		
Eucnide rupestris (Baillon) Thompson & Ernst	*n* = ca. 21	MEX, Baja California, S of La Ventana between Mexicali and San Felipe, *Rebman 2091* & *Hirales* (ASU).
Mentzelia multiflora (Nutt.) A. Gray	*n* = 10	USA, Arizona. Yavapai Co.: S of Ash Fork, 6 km SSE of Rock Butte, *Baker 11394.1* (ASU, two sheets).
Myrtaceae		
**Mosiera ehrenbergii* (Berg) Landrum	2*n* = 22	MEX, S.L.P.: Guadalcazar; cultiv. in ASU Greenhouse, Tempe, *Landrum 7375* (ASU). [JHC]
Polygonaceae		
**Eriogonum ripleyi* J.T. Howell	*n* = 16	USA, Arizona, Yavapai Co.: NW of Jerome, 4.2 km SSE of Red Butte, *Baker 11803* & *Wright* (ASU).
Portulacaceae		
**Phemeranthus validulus* (Greene) Kiger [*Talinum validulum* Greene]	*n* = 24	USA, Arizona, Yavapai Co.: ca. 9 km W of Jerome, W base of Woodchute Mtn., *Baker 9388* (ASU).
Rosaceae		
**Ivesia multifoliolata* (Torr.) Keck	*n* = 14	USA, Arizona, Coconino Co.: T19N R3E S15, Tule Tank Wash, *Baker 9847*.
***Prunus virginiana* L. var. *demissa* (Nutt.) Torr.	*n* = 16	USA, Arizona, Yavapai Co.: Woodchute Wilderness Area, 5 km NW of Jerome, *Baker 9823* (ASU, two sheets, second collection from same individual). Previously counted as 2*n* = 16 (Wilken 1993).
Scrophulariaceae		
Penstemon superbus A. Nelson	*n* = 8	USA, Arizona, Graham Co.: 2 km NNW of Solomon Pass W of Rock Tank, *Baker 11626* & *Kertell* (ASU).
Penstemon albomarginatus M.E. Jones	*n* = 8	USA, California, San Bernardino Co.: N34.8145E W116.4065E, 55 km W of Barstow, *Baker 16674.1* & *Silverman* (ASU).
	MONOCOTYLEDONAE	
Agavaceae		
Agave ×*arizonica* Gentry & J. H. Weber, pro sp. (*A. chrysantha* Peebles × *A. toumeyana* var. *bella*)	*n* = 30	USA, Arizona: cultiv. in Desert Botanical Garden, Arizona (Bed #40), *Hodgson 4526* (ASU, DES). [MB]

Table 1. (continued)

Taxon	Chromosome number	Locality, notes
	MONOCOTYLEDONAE	
Agave aff. *chrysantha* Peebles	*n* = 30	USA, Arizona, Yavapai Co.: 5 km N of Camp Verde, just W of Montezuma Castle Natl. Mon. boundary, *Baker 11854* et al. (with morphological intermediacy to *A. delamateri* Hodgson & Slauson (ASU, DES).
Agave felgeri Gentry	*n* = 30	MEX, Sonora: San Carlos Bay, *Felger 637* [topotype] (ASU, DES). [AS]
Agave glomeruliflora (Engelm.) A. Berger	*n* = 60	MEX, Coahuila, Los Cojos Minas, SW of limestone slopes of Sierra del Carmen, Gentry & Engard s.n., since cultiv. in Desert Bot. Gard., Arizona (DBG 1972-0159-01-07), *Hodgson 10196* (DES). [MB]
Agave margaritae Brandegee	*n* = 30	MEX, Baja Calif. Sur: Santa Margarita Island, *Glass s.n.* et al. [topotype] (DES). [AS]
**Agave mckelveyana* Gentry	*n* = 30	USA, Arizona, Yavapai Co.: 15 km SW of Bagdad, *Baker 10813* (ASU, DES); Rugar Ranch, SW of Kirkland Jct., W of Hwy. 89, N34E 21.765'W112E 44.816', *C.D. Avis s.n. et al.* (DES). [AS & Turcott]
Agave toumeyana Trel. var. *bella* Breitung	*n* = 30.	USA, Arizona, Yavapai Co.: ca. 5 km N of Camp Verde, *Wright 1538* et al.(ASU) [MB]
Agave utahensis Engelm. var. *kaibabensis* (McKelvey) Gentry	*n* = 30	USA, Coconino Co.: Grand Canyon Natl. Pk., E of Hance Creek, *Hodgson 9725* (DES). [MB]
Yucca glauca Nutt.	*n* = 30	USA, New Mexico, Colfax Co.: N36.781° W104.861°, *Baker 12530* & *Wright* (ASU, DES).
Nolinaceae		
Nolina bigelovii (Torr.) S. Watson	*n* = 19	USA, Arizona, Mohave Co.: Devil's Canyon, 15 km S of Wickieup, *Baker 10764* et al.. Yavapai Co.: 15 km SW of Bagdad, *Baker 10814* (ASU).

ACKNOWLEDGMENTS

Michael Chamberland, Tucson Botanical Garden and Wendy Hodgson, Desert Botanical Garden, Phoenix, provided collections and bud material for some of the chromosome determinations. Gerald D. Carr and L.M. Hill offered helpful comments on an earlier draft of the manuscript.

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BOOK NOTICE

Gabriela G. Hässel de Menéndez and Marta F. Rubies. 2009. **Catalogue of Marchantiophyta and Anthocerotophyta of southern South America (Nova Hedwigia, Beiheft 134).** (ISBN 978-3-443-51056-5, ISSN 1438-9134, pbk.). J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Johannestr. 3A, D-70176 Stuttgart, Germany. (**Orders:** www.schweizerbart.com, mail@schweizerbart.de, +49 (0)711 35 14 56 0, +49 (0)711 35 14 56 9 fax). $255.00, 672 pp., 3 b&w figures, 6 5/8" × 9 1/2".

Countries covered are Chile, Argentina and Uruguay, including Easter Island (Pascua Island), Malvinas Island (Falkland Island), South Georgia Island, and the subantarctic South Shetland Island, South Sandwich Island, and South Orkney Island.

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Index (42 pp. of scientific names)

From the introduction: "The present catalogue updates the information on the taxa known from Chile, Argentina, and Uruguay, and discusses erroneous data from old publications, mainly on the basis of modern literature and on studies by the senior author. The reasons to present a joint catalogue for these three southern South American countries are that the literature for Chile and Argentina is to a great extent the same, and Uruguay, although rather under collected [sic], has some phytogeographical relationship to Argentina, and could therefore not be left out."

ANATOMÍA DE LA EPIDERMIS FOLIAR EN LAS ESPECIES MEXICANAS DEL GÉNERO *MUHLENBERGIA* (POACEAE)

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RESUMEN

Se llevó a cabo un estudio comparativo de la anatomía de la epidermis abaxial en láminas foliares de 113 especies de *Muhlenbergia* de las 120 estimadas que habitan en México. Se identificaron 21 caracteres cruciales y fueron sometidos a un análisis de similitudes del que resultaron tres grupos principales, donde se observó la formación de subgrupos similares a los propuestos por otros autores con base en caracteres morfológicos. Con base en la similitud de especies, se infiere que posiblemente los caracteres morfológicos del género evolucionaron en forma paralela a los epidérmicos, este paralelismo no se observa con los caracteres anatómicos de sección transversal de lamina foliar, dado que no existe concordancia con la división del género en los subgéneros *Muhlenbergia* y *Trichochloa*, realizada con base en anatomía de sección transversal de laminas en la mayoría de las especies del género *Muhlenbergia*. El perfil de caracteres anatómicos de epidermis abaxial no parecen ser únicos para cada especie, siendo significativos para la separación de grupos de especies. Se presentan microfotografías y se describen los caracteres epidérmicos en la superficie abaxial que caracterizan al género y a grupos con especies similares.

Palabras Clave: Anatomía de epidermis, *Muhlenbergia*, Poaceae, México

ABSTRACT

A leaf epidermal survey on the abaxial surface was conducted to gather critical data for interpreting relationships among 113 species of *Muhlenbergia* from Mexico. Phenetic analyses using 21 crucial characters, support recognition of three major species groups. These three major species groups are concordant with previously reported groups based on morphological characters, while some are not concordant with the proposed subgenera: *Muhlenbergia* and *Trichochloa*, based on leaf anatomical characters of transversal sections. A profile of epidermal characters seems not to be unique for each species, but more characteristic for groups. Descriptions and photographs of the main characters are given for the genus and groups of similar species.

Key Words: Epidermal anatomy, *Muhlenbergia*, Poaceae, Mexico

INTRODUCTION

Las especies del género *Muhlenbergia* Schreb. (Chloridoideae, Eragrostoideae) se localizan desde cerca del nivel del mar hasta los límites alpinos, se distribuyen en regiones áridas y semiáridas del Nuevo Mundo desde el sur de Estados Unidos de América hasta Argentina; siete especies se encuentran en Asia. La mayoría de las especies (147 aprox.) se distribuyen en el sur de Norteamérica, por esta razón, el sur de Estados Unidos y México, se consideran como su posible centro de origen (Peterson y Herrera 2001).

El género *Muhlenbergia* comprende aproximadamente 160 especies en el Mundo, en México cuenta con cerca de 120 especies. Forma parte de los ecosistemas templados y secos con vegetación primaria de pastizales, matorrales xerófilos y bosques de encino y pino (Peterson y Herrera 2001). Es uno de los géneros de gramíneas con mayor importancia económica para México por su alto valor forrajero, amplia distribución y adaptabilidad. Las principales contribuciones al conocimiento sistemático parcial del género son los estudios realizados por: Soderstom (1967), Morden y Hatch (1987), Peterson y Annable (1991), Herrera y Grant (1994), Herrera (1998), Peterson (2000), Peterson y Herrera (2001) y Herrera y Peterson (2006).

El género *Muhlenbergia* se caracteriza por presentar especies anuales o perennes; las especies perennes son cespitosas, rizomatosas, o a veces decumbentes y enraizadas en los nudos inferiores (Herrera y Peterson

2006). Hitchcock (1951), en sus estudios florísticos de las especies americanas, define que estos caracteres morfológicos son de gran ayuda para dividir al género en grandes grupos y de esa manera hacerlo más manejable, separando *Muhlenbergia* en cuatro grandes grupos morfológicos: 1) Las especies anuales, pequeñas y frágiles; 2) Las especies perennes rizomatosas; 3) Las especies perennes no rizomatosas, robustas, mayores de 1.5 m de alto y 4) Las especies perennes no rizomatosas, no robustas, menores de 1 m de alto.

Peterson y Herrera (2001) en un estudio de anatomía foliar en sección transversal de las casi 160 especies conocidas en el Mundo del género *Muhlenbergia*, concluyen que el género es divisible en cuatro grupos anatómicos mayores correspondientes a dos subgéneros (*Muhlenbergia* y *Trichochloa*) y dos secciones (*Epicampes* y *Podosemum*) en el subgénero *Trichochloa*, y proponen el reconocimiento de estas entidades subgenéricas.

Estudios anatómicos de la epidermis abaxial de laminas han aportado información de calidad para la clasificación de las gramíneas en diferentes niveles como son: Metcalfe 1960; Renvoize 1981, Stieber 1982; Morden y Hatch 1987; Peterson y col. 1989; Gómez y Koch 1998; Vieria y col. 2002; Gómez y Téllez 2008. Por esta razón se estudiaron las especies mexicanas del género *Muhlenbergia* para determinar si los caracteres de la epidermis abaxial de lámina son consistentes en la delimitación de especies, así como para obtener caracteres "diagnóstico" que permitieran inferir sus relaciones de similitud.

MATERIALES Y MÉTODOS

Las muestras biológicas de las especies de *Muhlenbergia* (ver Apéndice) provienen principalmente de ejemplares depositados en los herbarios CIIDIR y UAA. Otras muestras proceden de los herbarios: ENCB, GUADA, IBUG, INEGI, MEXU, SLPM, TAES y US.

Para obtener fragmentos de epidermis abaxial, se utilizó la técnica de raspado directo, sobre la superficie adaxial en la porción media de láminas foliares bien desarrolladas, observando a través del microscopio estereoscópico. Los fragmentos se colocaron en una solución acuosa de detergente comercial y se llevaron a temperatura de ebullición durante 30 minutos para hidratar y ablandar los tejidos, en seguida se procedió a raspar la superficie adaxial, con navaja bisturí, para eliminar tejidos y obtener la epidermis abaxial limpia. Las muestras de epidermis se tiñeron con safranina y se eliminó el exceso de agua pasando los cortes por una solución acuosa de alcohol a diferentes concentraciones (30%, 50%, 70% 95% y 100%). Las muestras se montaron en resina.

Las observaciones anatómicas se hicieron con un microscopio de luz con objetivo de 10× y 40× y ocular de 10× de aumento, las microfotografías se tomaron con una cámara digital Canon Powershot S45 adaptada a un microscopio Leica DMD. Las descripciones de la epidermis abaxial se hicieron siguiendo la terminología propuesta por Ellis (1979).

El número de ejemplares analizados por especie fue variable (1 a 7, ver Apéndice), dependiendo de la abundancia o rareza y disponibilidad de cada especie. Así, de las especies menos comunes solo fué posible obtener una población para el presente análisis. En el caso de especies con distribución amplia se escogieron ejemplares de localidades distantes. La información de epidermis generada para cada especie se sometió a un análisis de similitudes. En el análisis cada especie (Apéndice), se consideró como una unidad taxonómica operacional (UTO) y se registraron 21 caracteres anatómicos de epidermis (Cuadro 1). Se aplicó el Índice de Euclidean (adecuado para el tipo de caracteres) con el fin de generar la matriz de similitudes a partir de la cual se construyó el árbol de similitudes o dendrograma mediante la utilización de UPGMA (unweighted pair group mathematical average clustering analysis).

RESULTADOS

Los resultados se interpretaron en dos formas: 1) la descripción general que se generó combinando los caracteres de todas las especies de *Muhlenbergia* incluidas en este estudio y 2) resultados de un análisis de similitudes.

Cuadro 1. Lista de caracteres y estados de carácter anatómicos en el análisis de conglomerados.

Carácter	Estados	Codificación
1. Diferenciación de zonas	Zonas costales e intercostales bien definidas	1
	Zonas costales e intercostales no definidas	2
2. Pared anticlinal de las células largas intercostales	Sinuosa	1
	Lisa	2
	Ondulada	3
3. Forma de las sinuosidades	Forma de U	1
	Forma de V	2
	Forma de	3
4. Hileras de estomas	Una hilera definida	1
	Dos hileras definidas	2
	Una hilera definida y algunos estomas dispersos	3
	Mas de dos hileras	4
5. Células cortas intercostales	Presentes	1
	Ausentes	0
6. Micropelos cantidad por campo	De 1 a 5	1
	De 6 a 10	2
	Más de 10	3
7. Micropelos (longitud total)	Hasta 9	1
	De 10 a 20	2
	Más de 20	3
8. Longitud célula basal micropelo	Menos de 5	1
	De 5 a 10	2
	Más de 10	3
9. Longitud célula apical micropelo	Hasta 12	1
	De 13 a 40	2
10. Papilas	Presentes	1
	Ausentes	0
11. Distribución de las papilas	Presentes en todas las células largas intercostales	1
	Presentes en las células ineterestomáticas	2
12. Arreglo de las papilas	Una papila por célula	1
	Más de una papila por célula	2
13. Papilas cubriendo al estoma	Una papila cubriendo en parte o en su totalidad al estoma	1
	Más de una papila rodeando al estoma	2
14. Forma de las papilas	Convexas e infladas	1
	Pequeñas y cóncavas	2
	Alargadas, distalmente engrosadas	3
15. Aguijones	ausentes	0
	presentes	1
16. Distribución de aguijones	En zonas intercostal	1
	En zonas costal	2
	En ambas zonas	3
17. Tamaño de la base del aguijón con respecto a la barba	Base más corta que la barba	1
	Base más larga que la barba	2
18. Forma de la barba en relación a la base	Barba desarrollada desde la base hasta el ápice altamente elevado	1
	Barba no desarrollada desde la base hasta el ápice, base cónica no elevada	2
19. Longitud de la barba en relación a la longitud de la base	Longitud de la barba más corta que la longitud de la base	1
	Longitud de la barba mucho más larga que la longitud de la base	2
20. Descripción de los cuerpos de sílice	Equidimensional, en forma de silla de montar, constreñidos en la porción central	1
	Equidimensional, en forma de silla de montar, redondeados, formando una doble equis	2
21. Macropelos	Presentes	1
	Ausentes	0

DESCRIPCIÓN GENERAL DE LA EPIDERMIS ABAXIAL EN LÁMINAS FOLIARES DE *MUHLENBERGIA* DE MÉXICO

Zonas Costal e intercostal.—(Fig. 1). La epidermis en vista de superficie, esta dividida en zonas o bandas conspicuas (Vieira y col. 2002). En las especies mexicanas del género *Muhlenbergia*, 103 especies presentan las zonas bien definidas, mientras que en las 10 restantes no es posible diferenciar estas dos zonas.

Células largas intercostales.—(Fig. 2). En las especies de *Muhlenbergia* las células largas intercostales presentan paredes anticlinales de tres tipos: Grupo I) 85 especies exhiben paredes sinuosas, 39 de ellas en forma de U, otras 36 en forma de V y las 11 especies restantes en forma de. Grupo II) 12 especies con paredes lisas y Grupo III) 16 especies con paredes onduladas (Ellis 1979).

Estomas.—En todas las especies examinadas se observaron aparatos estomáticos subdiscoidales. Las células subsidiarias son redondeadas (en forma de domo), en una, dos o más hileras longitudinales a lo largo de la zona intercostal.

Papilas.—(Fig. 3). La superficie externa de las células epidérmicas son aplanadas o convexas o presentan abultamientos o salientes conocidos como papilas. Estas salientes de la pared externa pueden ser muy diferentes, desde las simples cónicas a estructuras más largas, localizadas en el centro o en la parte distal de las células intercostales largas, de acuerdo con Ellis (1979), las especies de *Muhlenbergia* presentan formas convexas e infladas, pequeñas y hundidas, alargadas distalmente engrosadas.

Tricomas.—Las especies de *Muhlenbergia*, en su epidermis abaxial muestran dos tipos de tricomas: Micropelos y Aguijones.

Micropelos.—(Fig. 4). Los micropelos consisten de dos células con paredes delgadas, una célula basal y una distal. Las células del micropelo en conjunto pueden ser más largas o pueden ser más cortas que el complejo estomático. En el presente estudio la mayoría de las especies presentan micropelos con una longitud total de hasta 20. Se distinguieron 2 tipos característicos: i) célula distal inflada, de 1/3 ó 2/3 del largo del micropelo, sin célula apical (Figs. 5a y 5b); ii) célula distal delgada (no inflada), 1/3 ó 2/3 del largo del micropelo, con una célula apical corta (1/10 del largo del micropelo) o carente de ella. Pocas especies poseen micropelos con una longitud total mayor a 20, su forma característica es ser micropelos delgados y alargados con la célula apical más corta que la distal, (Figs. 5c y 5d).

Aguijones.—(Fig. 5). Los aguijones son fitolitos unicelulares, que se distinguen por su base dilatada y el ápice afilado, se observan en la zona costal, en la zona intercostal, en ambas zonas o pueden estar ausentes. De las especies estudiadas 56 tienen aguijones en la zona costal, 4 en la zona intercostal, 13 en ambas zonas y 40 no presentan aguijones.

Células Cortas.—(Fig. 6). Las células cortas se dividen en células de sílice cuando el interior de la célula esta ocupado por SiO_2 que se solidifica en formas variadas, y son llamados cuerpos de sílice. El otro tipo de células cortas son denominadas células de corcho o súber, cuyas membranas están suberificadas y a menudo tienen material orgánico sólido. La mayoría de las especies mexicanas del género *Muhlenbergia* (96 especies) contienen cuerpos de sílice del tipo de silla de montar formando una doble equis, y las 17 restantes con cuerpos de sílice en forma de silla de montar constreñidos en la parte media con los extremos redondeados o irregulares (Figs. 6a y 6b). Los cuerpos de sílice se localizan en las zonas costales. El otro tipo de celdas son las células de corcho que se encuentran tanto en la zona costal como en la intercostal, sin embargo en las especies estudiadas son raras en las zonas intercostales y comunes en la zona costal (Fig. 6d). Las células cortas se agrupan en hileras longitudinales ya sea en pares o solitarias, (Figs. 6c y 6d) entre células largas consecutivas.

Macropelos.—(Fig. 7). Los macropelos generalmente se disponen en la zona intercostal de la epidermis. Solo en 18 de las especies estudiadas se observaron macropelos. Éstos son de diferentes tamaños desde pequeños con un ápice punzante hasta largos y suaves al tacto como los que muestra *M. pubescens*.

La epidermis de las láminas foliares, en vista de la superficie abaxial, esta dividida en zonas o bandas conspicuas. En general es posible distinguir dos zonas principales la zona costal y la zona intercostal. La mayoría de las especies mexicanas de *Muhlenbergia* presentan esta organización, sin embargo, especies tales

como, *M. alamosae, M. capillipes, M. densiflora, M. dubia, M. firma, M. glabrata, M. gypsophila, M. laxiflora, M. macroura* y *M. nigra* no presentan diferenciación de dichas zonas. En estos casos, la descripción de caracteres epidérmicos se lleva a cabo localizando sus estomas y micropelos que son típicos de la zona intercostal.

ANÁLISIS FENÉTICO

En las especies analizadas (Cuadro 1) se determinaron 21 caracteres epidérmicos de calidad taxonómica (diagnóstico). Dichos caracteres fueron utilizados para hacer una matriz (Cuadro 2) la cual se sometió a un análisis de similitudes. El dendrograma resultante (Fig. 14) reveló la existencia de tres grupos principales definidos por: la presencia/ ausencia de aguijones, la presencia/ ausencia de papilas, además de *M. breviseta* y *M. hintonii* en una posición externa a ellos. El grupo I incluyó 47 especies que muestran aguijones y carecen de papilas, en el grupo II se agruparon 27 especies que muestran tanto aguijones como papilas, y en el grupo III se concentran 37 especies sin papilas ni aguijones. Las 2 especies externas (*M. breviseta* y *M. hintonii*) comparten con el grupo 3 la carencia de papilas y de aguijones.

Las especies del grupo I (Fig. 14) incluyen aquellas que tienen bien definidas las zonas costales e intercostales, aguijones principalmente en la zona costal y ausencia de papilas; se redefinen en subgrupos: el subgrupo IA se define por la presencia de una sola hilera de estomas en la zona intercostal (Fig. 8), mientras que el subgrupo IB lo conforman las especies que presentan dos o mas hileras de estomas por zona intercostal (Fig. 9).

El grupo II (Fig. 14) esta integrado por especies que tienen papilas, aguijones, zonas costales e intercostales bien definidas, estomas en una, dos o más hileras, mientras que son del grupo de plantas perennes, no robustas. También se forman claramente dos subgrupos: el subgrupo IIA contiene 10 especies que disponen de papilas y aguijones y la mayoría no presenta sinuosidades en las paredes anticlinales de las células largas intercostales (Fig. 10). El subgrupo IIB contiene 16 especies que disponen de papilas y aguijones y además muestran sinuosidades en forma de U o de V en las paredes anticlinales del las células largas intercostales (Fig. 11).

El grupo III que se define por carecer de aguijones y de papilas, se divide en dos subgrupos: IIIA con la mayoría de las especies anuales (Fig. 12), y IIIB con la mayoría de las especies perennes de vida corta (Fig. 13). Las especies que son externas a los grupos en el dendrograma, se asocian más con el tercer grupo por compartir con este la carencia de aguijones y papilas.

DISCUSIÓN

En el grupo I (Fig. 14) se concentran especies perennes, la mayoría de ellas robustas, con algunas intrusiones de especies no robustas, compartiendo los caracteres de epidermis abaxial anotados.

En el grupo II (Fig. 14) dominan especies perennes no robustas y rizomatosas por igual. Es interesante observar que en el subgrupo IIB comprende ocho de las 13 especies del complejo *Muhlenbergia montana* incluidas en este estudio (*M. cualensis, M. eriophylla, M. jonesii, M. michisensis, M. virescens, M. quadridentata, M. montana* y *M. watsoniana*), reconocido por Herrera y Grant (1994), con base en caracteres morfológicos, anatómicos foliares de sección transversal y del contenido de flavonoides. Como se observa en el dendrograma (Fig. 14), estas especies son también similares con base en anatomía de epidermis abaxial.

El grupo III esta constituido a su vez por dos subgrupos: el subgrupo IIIA formado por especies que no presentan papilas ni aguijones (Fig. 14); especies la mayoría de hábitos anuales. Mientras que en el subgrupo IIIB con presencia de papilas y ausencia de aguijones, se encuentran en mezcladas especies perennes rizomatosas, estoloníferas decumbentes y anuales en proporciones similares.

Las observaciones anteriores muestran la concordancia que presentan las especies de *Muhlenbergia* en sus caracteres morfológicos vegetativos y epidérmicos en vista de superficie abaxial. Así, encontramos que especies cercanas morfológicamente como *M. texana* y *M. eludens* (por caracteres de lema y cariopside), anatómicamente también son similares (misma rama en Fig. 14). Sin embargo, el caso contrario también sucede, donde especies como *M. rigens* y *M. aguascalientensis* morfológicamente son muy disimiles, mientras que por su epidermis, presentan caracteres similares que las coloca mas cerca entre sí que con otras especies.

Cuadro 2. Matriz básica de datos.

UTOs	E. Carácter																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
M. aguascalientensis	1	1	2	1	1	1	2	3	1	0	0	0	0	0	1	2	2	2	1	2	0
M. alamosae	2	2	2	1	0	1	2	3	1	1	1	0	2	1	3	2	2	1	1	2	0
M. annua	1	1	3	2	0	2	2	2	2	0	0	0	0	0	0	0	0	0	0	2	0
M. appressa	1	3	0	1	1	2	1	2	1	0	0	0	0	0	2	1	2	2	1	2	0
M. arenacea	1	1	2	4	1	1	2	2	2	1	1	1	0	3	0	0	0	0	0	2	0
M. arenicola	1	2	0	2	0	1	2	2	1	1	1	2	2	3	0	0	0	0	0	2	1
M. argentea	1	1	2	2	0	1	2	3	2	1	1	1	0	1	1	2	2	2	1	2	0
M. arizonica	1	3	0	4	0	2	2	2	1	1	2	1	0	1	0	0	0	0	0	2	0
M. arsenei	1	2	0	2	0	1	2	2	1	1	1	2	2	3	0	0	0	0	0	2	1
M. articulata	1	1	2	2	0	2	2	2	2	0	0	0	0	0	1	2	2	2	1	2	0
M. asperifolia	1	1	2	2	1	1	2	2	2	1	1	1	2	0	0	0	0	0	0	2	0
M. brandegei	2	2	0	1	0	1	2	2	1	1	1	1	0	1	0	0	0	0	0	2	1
M. brevifolia	1	1	1	2	1	1	2	1	2	1	2	1	0	3	1	2	1	1	2	2	0
M. breviligula	1	3	0	4	0	1	2	3	1	0	0	0	0	0	1	2	2	1	1	2	0
M. brevis	1	1	3	2	0	1	2	2	2	1	2	1	1	3	1	2	2	2	1	2	1
M. breviseta	1	1	2	4	0	2	1	5	1	0	0	0	0	0	0	0	0	0	0	2	0
M. brevivaginata	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	2	2	1	2	2	1
M. capillaris	1	1	2	1	0	1	2	2	1	0	0	0	0	0	1	2	2	2	1	2	0
M. capillipes	1	1	3	2	1	3	1	1	1	1	1	1	1	1	0	0	0	0	0	2	1
M. ciliata	1	1	3	1	1	2	2	2	2	0	0	0	0	0	0	0	0	0	0	1	1
M. confusa	1	1	3	2	0	3	2	2	2	0	0	0	0	0	0	0	0	0	0	1	0
M. crispiseta	1	3	0	2	0	1	2	3	2	1	1	1	3	0	0	0	0	0	0	2	0
M. cualensis	1	1	2	2	0	1	1	1	1	1	1	2	2	3	1	2	2	2	2	2	0
M. curvula	1	1	2	2	0	1	2	2	2	0	0	0	0	0	1	1	2	2	1	2	0
M. densiflora	2	1	2	1	0	1	2	3	2	0	0	0	0	0	1	2	2	2	1	2	0
M. depauperata	1	1	2	4	1	2	1	1	2	1	1	1	0	3	0	0	0	0	0	2	1
M. distans	1	1	2	4	0	3	2	3	1	0	0	0	0	0	1	2	2	2	1	2	0
M. distichophylla	1	3	0	4	0	1	2	3	2	0	0	0	0	0	1	3	2	2	1	2	0
M. diversiglumis	1	3	0	1	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0	1	1
M. dubia	2	1	2	0	0	0	0	0	0	0	0	0	0	0	1	3	2	2	2	2	0
M. dumosa	1	2	0	2	0	2	1	2	1	1	1	2	2	3	1	3	2	1	2	2	0
M. durangensis	1	1	1	2	0	2	1	2	1	0	0	0	0	0	1	3	2	2	1	2	0
M. elata	1	1	1	4	0	2	2	2	2	0	0	0	0	0	1	2	2	2	1	2	0
M. elongata	1	1	1	2	0	2	1	2	1	0	0	0	0	0	1	2	2	1	1	2	0
M. eludens	1	1	1	2	0	1	2	1	2	0	0	0	0	0	0	0	0	0	0	2	1
M. emersleyi	1	1	1	4	0	3	2	3	1	0	0	0	0	0	1	2	2	1	1	2	0
M. eriophylla	1	1	1	2	0	1	1	1	1	1	1	2	2	3	1	2	2	2	1	2	0
M. firma	2	1	2	3	0	0	0	0	0	0	0	0	0	0	1	3	2	2	1	2	0
M. flavida	1	1	2	1	1	2	2	3	2	0	0	0	0	0	0	0	0	0	0	1	0
M. flaviseta	1	2	0	2	0	3	2	2	1	1	1	1	2	3	0	0	0	0	0	2	0
M. fragilis	1	1	1	3	1	2	3	3	2	0	0	0	0	0	0	0	0	0	0	2	0
M. gigantea	1	1	1	4	0	1	3	2	1	0	0	0	0	0	1	2	1	1	2	2	0
M. glabrata	2	1	2	0	1	1	1	2	1	0	0	0	0	0	1	3	2	2	1	2	0
M. glauca	1	1	2	2	0	2	2	3	1	1	2	1	1	3	1	2	2	1	2	2	0
M. gooddingii	1	1	2	4	0	2	2	3	1	0	0	0	0	0	1	2	1	1	2	2	0
M. grandis	1	1	2	4	0	1	2	2	1	0	0	0	0	0	1	2	2	2	1	2	1
M. gypsophila	2	1	1	0	0	0	0	0	0	0	0	0	0	0	1	3	1	1	2	2	1
M. hintonii	1	3	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
M. implicata	1	1	3	2	0	3	2	2	2	0	0	0	0	0	0	0	0	0	0	2	0
M. iridifolia	1	2	0	2	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0	2	0
M. jaliscana	1	3	0	4	0	1	1	2	1	0	0	0	0	0	1	3	2	2	2	2	0
M. jonesii	1	1	1	2	0	1	2	2	1	1	1	1	2	3	1	2	2	2	1	2	0

Cuadro 2. (continued)

	E. Carácter																				
UTOs	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
M. laxa	1	3	0	2	0	3	2	2	2	1	1	1	0	2	0	0	0	0	0	1	0
M. laxiflora	2	1	1	0	0	1	2	2	1	0	0	0	0	0	1	3	2	2	2	2	0
M. lindheimeri	1	3	0	2	0	0	0	0	0	0	0	0	0	0	1	2	2	2	1	2	0
M. longiglumis	1	1	1	2	0	1	1	2	1	0	0	0	0	0	1	2	1	1	2	2	0
M. longiligula	1	1	1	4	0	2	1	1	3	0	0	0	0	0	1	2	1	1	2	2	0
M. lucida	1	1	1	2	0	1	1	2	1	0	0	0	0	0	1	2	2	2	1	2	0
M. macrotis	1	1	2	4	0	1	2	3	1	0	0	0	0	0	1	3	2	1	1	2	0
M. macroura	1	1	1	2	1	0	0	0	0	0	0	0	0	0	1	2	1	1	2	2	0
M. majalcensis	1	2	0	4	0	1	2	3	1	1	2	1	0	1	0	0	0	0	0	2	0
M. michisensis	1	1	1	2	0	1	2	2	1	1	1	1	2	3	1	2	2	2	1	2	0
M. microsperma	1	2	0	2	0	2	2	3	2	1	1	1	0	2	1	2	1	1	2	2	0
M. minutissima	1	1	3	2	0	2	2	2	2	0	0	0	0	0	0	0	0	0	0	1	0
M. montana	1	1	1	2	0	2	1	2	1	1	1	1	2	3	1	2	1	1	2	2	0
M. monticola	1	2	0	2	0	1	2	2	1	0	0	0	0	0	1	2	1	1	2	2	0
M. mucronata	1	1	1	2	1	0	0	0	0	0	0	0	0	0	1	2	1	1	2	2	0
M. nigra	2	1	1	0	0	1	0	2	0	0	0	0	0	0	1	3	2	2	1	2	0
M. orophila	1	1	2	2	1	3	1	2	2	0	0	0	0	0	0	0	0	0	0	2	0
M. palmeri	1	1	2	1	1	1	2	2	1	0	0	0	0	0	1	2	2	2	1	2	0
M. parviglumis	1	3	0	1	0	2	2	3	1	1	1	1	0	3	1	2	1	1	2	2	0
M. pauciflora	1	1	2	1	1	1	2	2	1	0	0	0	0	0	1	2	2	2	1	1	0
M. pectinata	1	1	2	1	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0	1	1
M. peruviana	1	3	0	2	0	1	2	3	1	1	1	1	0	0	0	0	0	0	0	2	0
M. plumbea	1	1	1	2	1	1	2	2	2	1	1	1	0	3	0	0	0	0	0	2	0
M. polycaulis	1	3	0	2	1	2	2	2	1	1	2	1	1	3	1	2	1	1	2	2	0
M. porteri	1	3	0	2	0	1	2	3	1	1	1	1	0	1	1	2	2	2	1	2	0
M. pubescens	1	1	2	2	0	0	0	0	0	1	2	1	1	3	1	2	2	1	1	2	1
M. pubigluma	1	1	3	4	0	1	2	1	1	1	2	1	0	2	1	2	1	1	2	2	0
M. purpusii	1	3	0	2	0	2	2	2	2	1	2	1	1	3	1	2	1	1	2	2	0
M. quadridentata	1	1	2	2	0	1	2	2	1	1	1	2	2	3	1	2	2	2	1	2	0
M. ramulosa	1	1	1	1	1	2	2	2	1	0	0	0	0	0	0	0	0	0	0	1	0
M. reederorum	1	1	1	2	0	2	2	3	1	0	0	0	0	0	1	2	2	2	1	2	0
M. repens	1	1	1	2	1	1	3	2	2	1	1	1	1	3	0	0	0	0	0	2	0
M. richardsonis	1	1	2	2	1	1	2	2	1	1	1	1	2	3	0	0	0	0	0	2	0
M. rigens	1	1	2	1	1	1	2	3	1	0	0	0	0	0	1	2	2	2	1	2	0
M. rigida	2	1	2	1	1	1	1	2	1	0	0	0	0	0	1	2	2	2	1	2	0
M. robusta	1	1	2	2	1	2	2	2	1	1	1	1	0	3	1	2	2	2	1	2	0
M. schreberi	1	3	0	1	0	2	2	3	1	1	1	1	0	1	1	2	1	1	2	1	0
M. scoparia	1	1	1	2	0	2	0	2	1	0	0	0	0	0	1	2	2	1	1	2	0
M seatonii	1	1	1	1	0	3	2	2	2	0	0	0	0	0	0	0	0	0	0	1	0
M. setifolia	1	2	0	2	0	3	1	2	1	0	0	0	0	0	1	2	1	1	2	2	0
M. sinuata	1	1	1	4	0	2	2	2	2	0	0	0	0	0	0	0	0	0	0	2	1
M. sinuosa	1	1	1	2	0	2	1	2	2	1	2	1	1	3	0	0	0	0	0	2	1
M. speciosa	1	1	2	4	0	0	0	0	0	1	1	1	0	2	1	2	2	2	1	2	0
M. spiciformis	1	1	2	1	0	3	2	3	1	1	1	1	0	2	1	2	1	1	2	2	1
M. stricta	1	1	1	4	0	2	1	2	1	0	0	0	0	0	1	2	2	2	1	2	0
M. strictior	1	1	3	2	0	2	1	1	2	0	0	0	0	0	0	0	0	0	0	1	0
M. subaristata	2	1	1	1	1	1	2	3	1	0	0	0	0	0	1	3	2	2	1	2	0
M. tenella	1	1	3	1	0	1	2	2	1	0	0	0	0	0	0	0	0	0	0	1	1
M. tenuifolia	1	2	0	1	0	1	2	1	1	0	0	0	0	0	1	2	1	1	2	1	0
M. tenuissima	1	1	1	1	0	2	2	2	2	0	0	0	0	0	0	0	0	0	0	1	1
M. texana	1	1	1	2	0	1	2	1	2	0	0	0	0	0	0	0	0	0	0	1	1
M. torreyi	1	1	1	2	1	3	2	2	2	0	0	0	0	0	1	2	1	1	2	2	0

Cuadro 2. (continued)

	E. Carácter																				
UTOs	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
M. utilis	1	1	1	2	1	2	2	2	1	1	1	1	0	2	0	0	0	0	0	2	0
M. vaginata	1	1	1	2	1	2	2	3	2	1	1	1	0	1	0	0	0	0	0	2	0
M. versicolor	1	1	2	2	0	1	2	2	1	0	0	0	0	0	1	2	2	2	1	2	0
M. villiflora	1	1	1	2	3	3	3	2	1	1	1	1	0	2	1	1	1	1	1	1	0
M. virescens	1	1	1	2	0	1	2	3	1	1	1	1	2	3	1	2	2	2	1	2	0
M. virletii	1	1	2	4	0	1	3	1	1	0	0	0	0	0	1	2	2	1	1	2	0
M. watsoniana	1	1	3	2	0	1	1	2	1	1	1	1	2	3	1	3	1	1	2	2	0
M. wrightii	1	1	1	2	1	2	3	3	2	1	1	1	0	1	2	1	0	0	2	2	0
M. xanthodas	1	1	2	3	0	3	2	2	2	0	0	0	0	0	1	2	1	1	2	2	0

De los datos generados en las especies analizadas, se confirman las conclusiones obtenidas por Soderstrom (1967), en lo relativo a los micropelos y cuerpos de sílice de los grupos *Podosemum* y *Epicampes*, señalando que los micropelos del primer grupo son cortos y su célula distal es inflada (Fig. 4a), mientras que los del segundo grupo son más largos y delgados (Fig. 4d). En cuanto a los cuerpos de sílice el autor menciona que son del tipo de silla de montar formando una doble equis (Fig. 6b), este caracter de los cuerpos de sílice lo comparten las 113 especies estudiadas del género, mientras que, los micropelos de las especies que no se incluyen en estos dos grupos, presentan micropelos característicos de *Podosemum* o de *Epicampes* en cuanto a forma y tamaño.

De acuerdo con Ellis (1979), las papilas en la familia Poaceae, ocurren en las células largas y cortas, especialmente en las zonas intercostales, y el número puede variar de una a muchas por célula. En las especies estudiadas de *Muhlenbergia* la presencia o ausencia de papilas es un carácter importante para separar las especies en grupos (IIIa y IIIb, Fig. 14), lo que por otra parte, confirma la propuesta de Vieira y col. (2002), quienes señalan que la presencia o ausencia de papilas puede ser interpretado como un carácter de valor taxonómico.

Los aguijones o ganchos son estructuras epidérmicas a las que se les ha dado poca importancia, en algunos trabajos, sólo se menciona que son asperezas de la epidermis que se presentan tanto en la zona costal como intercostal (Vieira y col. 2002, Ellis 1979). Sin embargo, para las especies del género *Muhlenbergia* fueron importantes, ya que de acuerdo a la presencia, ausencia, forma y tamaño (ver en Cuadro1), se forman grupos definidos, por lo cual se consideran caracteres taxonómicos importantes en este género.

Las células cortas se presentan en pares o solitarias en hileras longitudinales, y se clasifican en células silíceas o suberosas de acuerdo al contenido del lumen (Vieira y col. 2002). Los cuerpos de sílice dentro de la célula silícea tienen formas características que han sido importantes para reconocer tribus o aun subfamilias de la familia Poaceae (Ellis 1979). En las especies mexicanas del género *Muhlenbergia* se presentan cuerpos de sílice del tipo característico en la subfamilia Chloridoideae, en forma de silla de montar formando una doble equis, aunque en algunas especies se presentan cuerpos de sílice más largos transversalmente con la parte media más estrecha y los extremos redondeados o irregulares, son también considerados por el mismo autor con forma de silla de montar.

La forma de estomas es otro carácter que se presenta en la epidermis. Los aparatos estomáticos son subdiscoidales, compuestos de células subsidiarias redondeadas (en forma de domo). Se encuentran distribuídos en dos hileras longitudinales, una hilera a cada lado de la zona costal. Este carácter igual que los cuerpos de sílice, son caracteres con valor taxonómico bajo por presentar formas con escasa variación en todas las especies, por tal motivo no ayudan a la separación de grupos.

Comparando los grupos obtenidos a partir de caracteres de epidermis abaxial en laminas de *Muhlenbergia* con los de anatomía foliar en corte transversal de *Muhlenbergia* (Peterson y Herrera 2001), no se observan

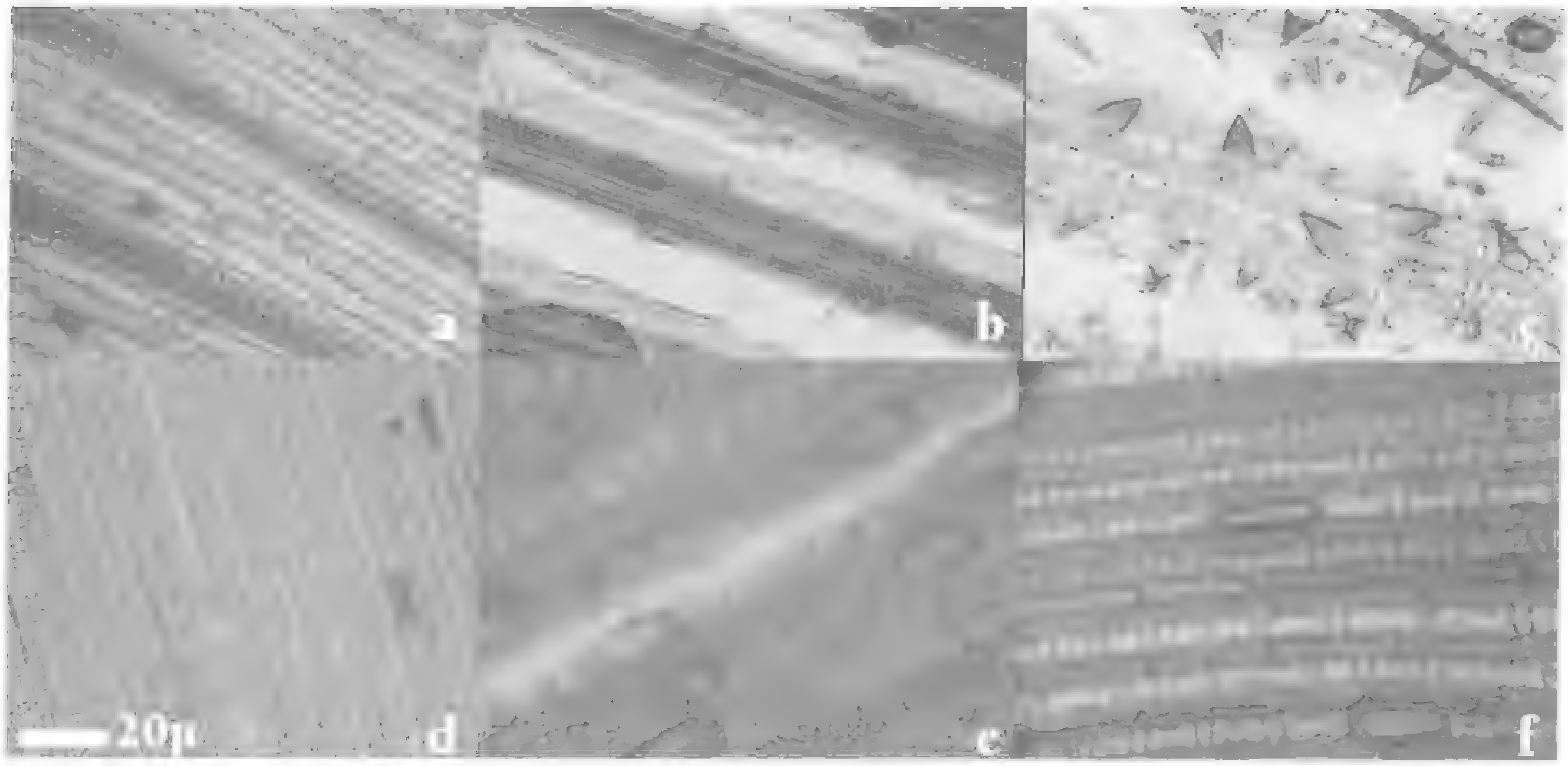

Fig. 1. Zonas Costales e Intercostales de la epidermis abaxial de *Muhlenbergia,* obtenidas por el método de raspado: (a–c) *M. ciliata, M. emersleyi* y *M. watsoniana* con zonas definidas, (d–f) *M. gypsophila, M. laxiflora* y *M. nigra* con zonas no definidas.

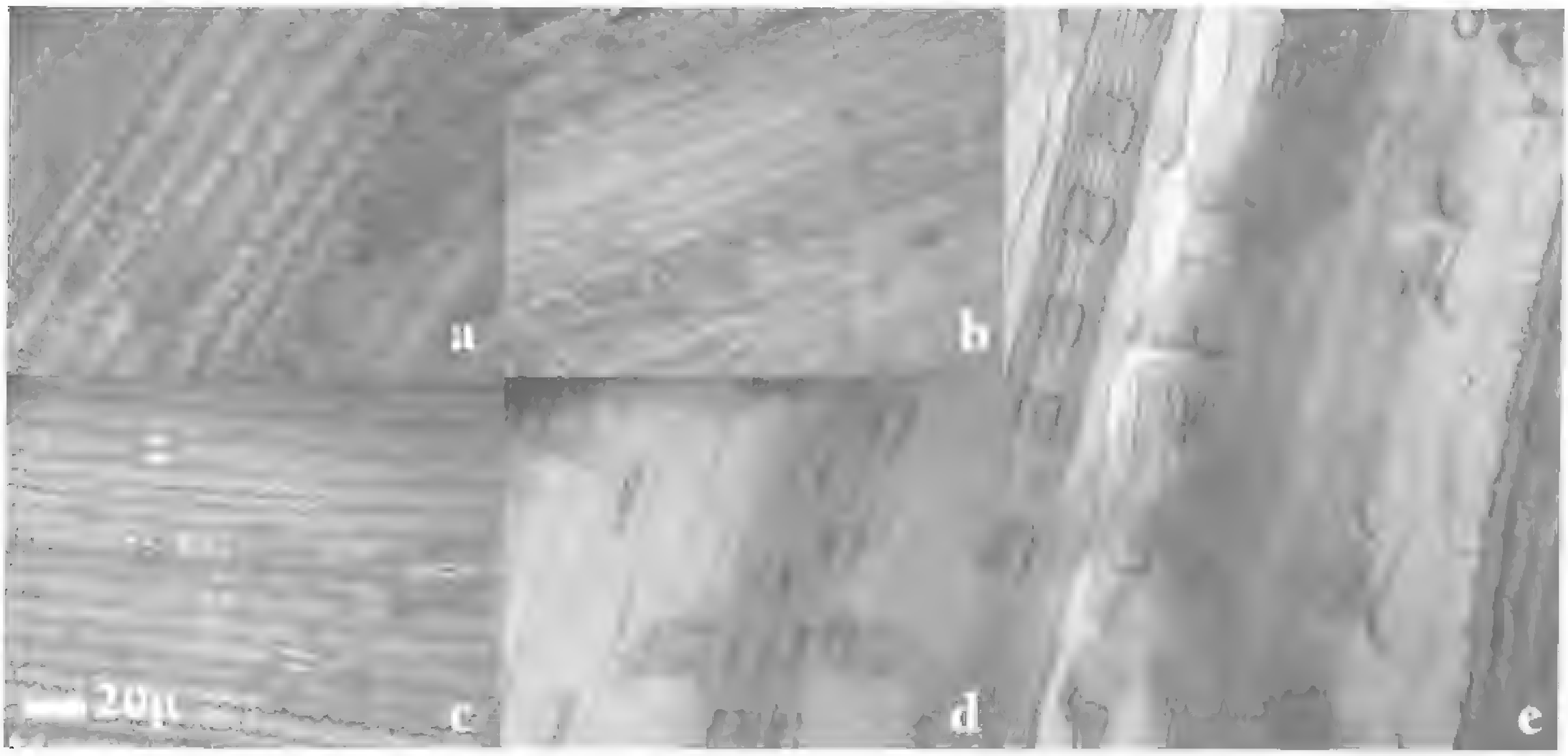

Fig. 2. Paredes Anticlinales Sinuosas de las células intercostales largas, obtenidas por el método de raspado: a) *M. annua*, sinuosidades en forma de U. b) *M. pectinata*, sinuosidades en forma de V. c) *M. ciliata*, sinuosidades en forma de W. d) *M. tenuifolia*. Paredes lisas, y e) *M. peruviana*, paredes onduladas.

similitudes con las agrupaciones naturales (emanadas de un análisis cladístico) que dieron sustento a la propuesta de reconocer los subgéneros (*Muhlenbergia* y *Trichochloa*) y las secciones (*Epicampes* y *Podosemum*) en el subgénero *Trichochloa*. El dendrograma de epidermis abaxial (Fig. 14) muestra que las especies de los subgéneros mencionados (Peterson y Herrera 2001) se intercalan en todos los grupos del dendrograma de caracteres epidérmicos. En el primer y segundo grupos, por ejemplo, se asocian especies tanto de *Muhlenbergia, Epicampes* y *Podosemum*. El tercer grupo está más definido, con la mayoría de las especies del subgénero *Muhlenbergia*, sin embargo, también se agregan especies de las secciones *Podosemum* y *Epicampes*.

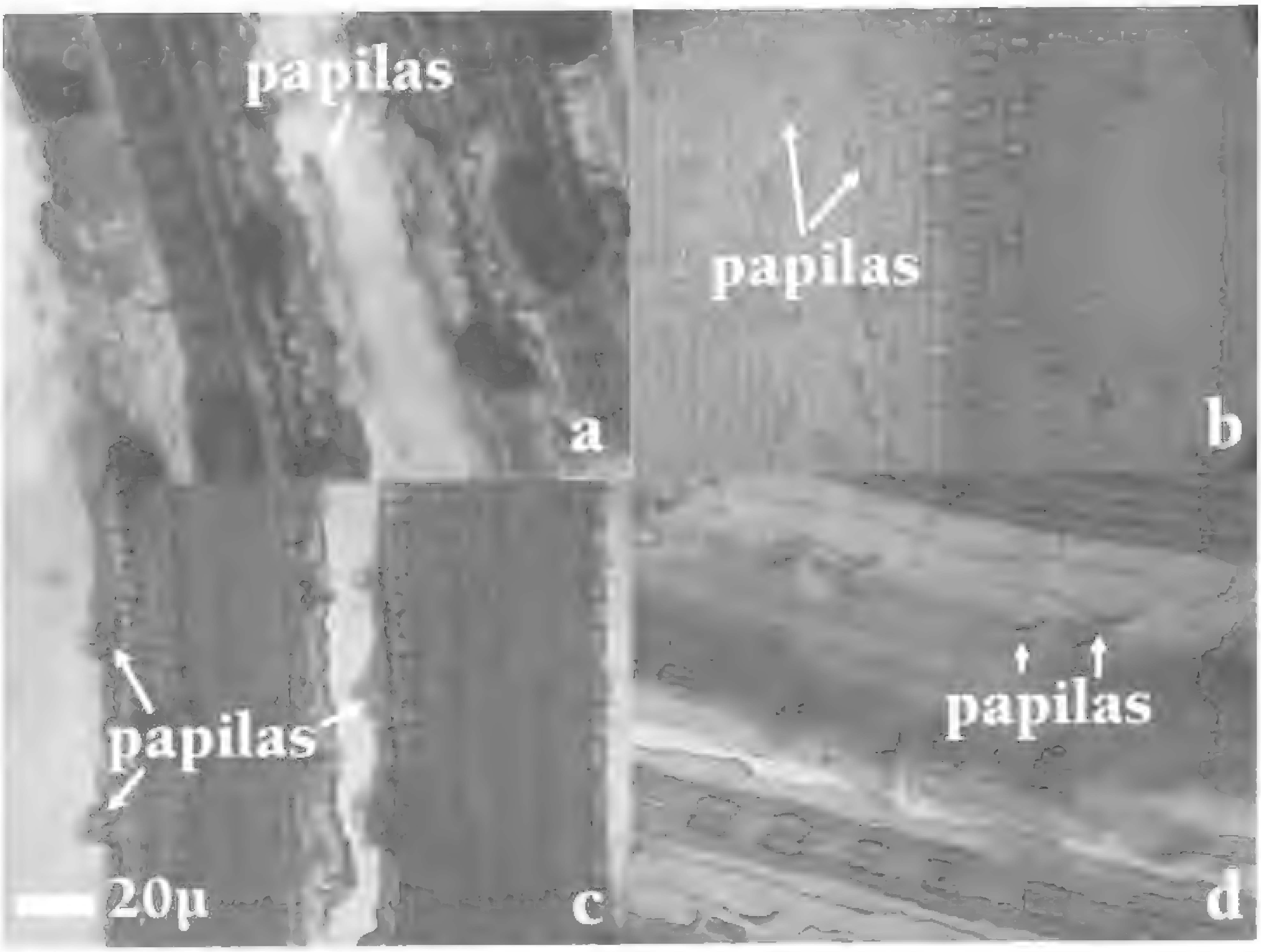

Fig. 3. Tipos de Papilas presentes en *Muhlenbergia*, obtenidas por el método de raspado: a) *M. glauca* con papilas alargadas cubriendo al estoma, b) *M. arenacea* con papilas hundidas, c) *M. flaviseta* con varias papilas cubriendo al estoma, d) *M. peruviana* con papilas convexas e infladas.

El presente estudio es el primero que se hace con base en la epidermis abaxial de las especies del género *Muhlenbergia* (Poaceae) de México, en el cual se estudiaron 113 de las cerca de 120 especies reportadas.

CONCLUSIONES

El conjunto de caracteres epidérmicos que exhiben las especies del género *Muhlenbergia* de México, demuestra que la epidermis por si sola no puede ser utilizada en la delimitación de especies, secciones y subgéneros de *Muhlenbergia*. Podrían ser considerados caracteres adicionales a los morfológicos y los anatómicos de corte transversal en láminas foliares, para la delimitación de especies.

De la formación de grupos epidérmicos diferentes a los anatómicos de sección transversal, en las especies del género *Muhlenbergia* de México, podría concluirse que la anatomía de epidermis foliar posiblemente tuvo una evolución divergente a la de sus estructuras internas.

APÉNDICE

Especimenes de *Muhlenbergia* utilizados en este estudio (colectores en negritas corresponden a las imágenes de las figuras 1–13).

M. aguascalientensis. Aguascalientes: Playa Mariquitas, 12 km al NW de la Congoja, mpio. San José de Gracia, *García, Herrera y de la Cerda 5531* (UAA); ***de la Cerda 1185* (UAA).**

M. alamosae. Aguascalientes: Barranca de los Lobos, Calvillo, *de la Cerda & O. Rosales 303* (UAA). Durango: Potrero la Tinaja, 2 km de San Juan de Michis por el camino La Michilía, Súchil, *Y.Y. Herrera 21* (CIIDIR). Jalisco: Arroyo del

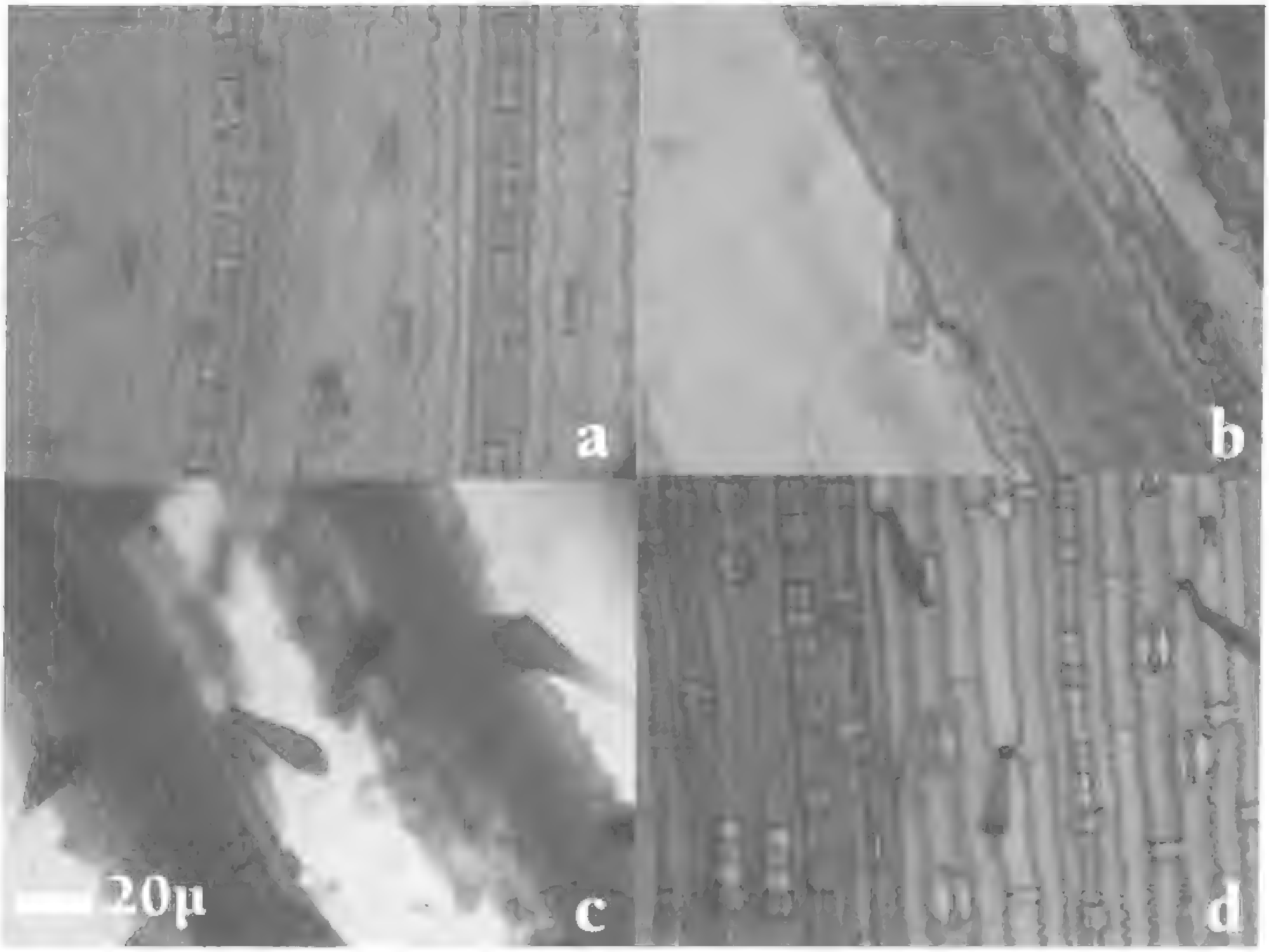

FIG. 4. Tipos de Micropelos, obtenidos por el método de raspado: **a)** *M. strictior*, pequeños e inflados < 30, b y c) 32 a 80, **b)** *M. flaviseta* micropelos inflados célula distal 1/3 del total, **c)** *M. quadridentata* micropelos angostos y alargados, célula distal 1/10 del total, **d)** *M. fragilis* micropelos angostos y alargados > 80.

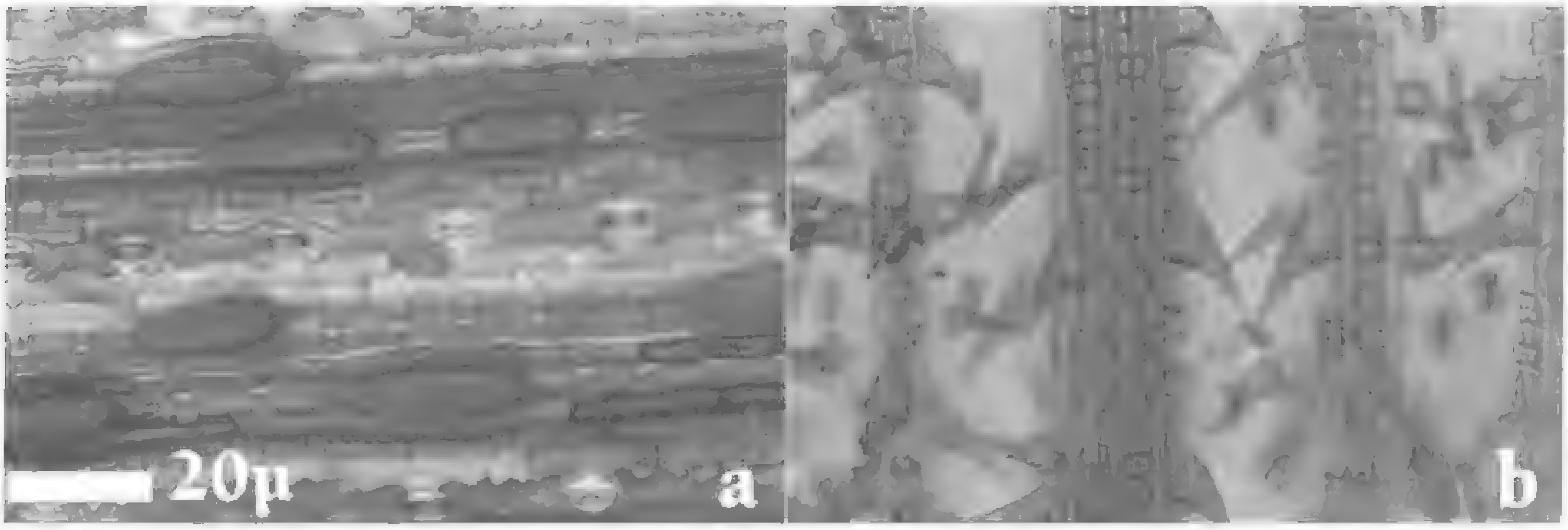

FIG. 5: Tipos de Aguijones, obtenidos por el método de raspado: **a)** *M. rigens* con aguijones de base mucho más larga que la punta, **b)** *M. brevifolia* con aguijones de punta mas larga que la base.

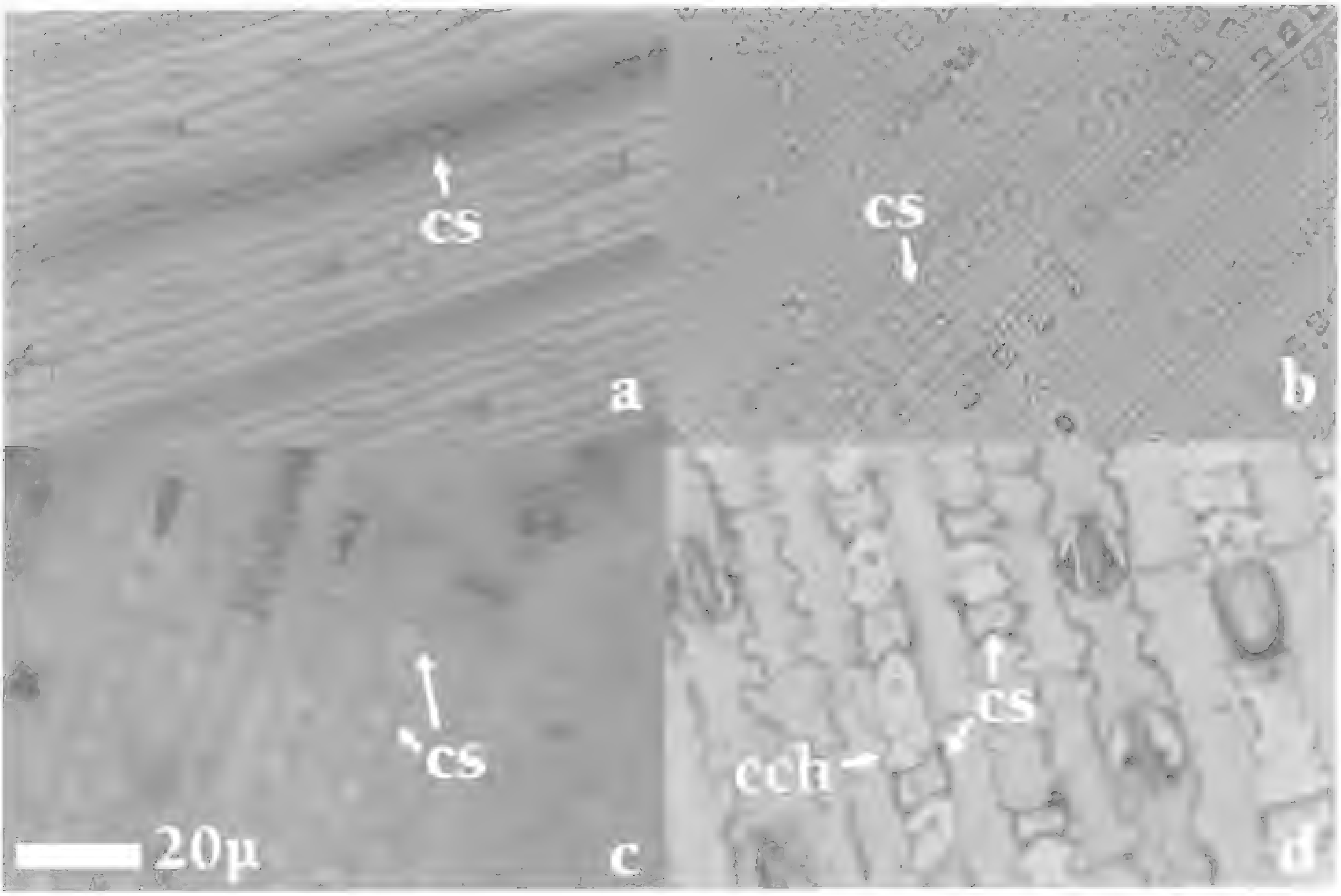

Fig. 6. Celulas Cortas, obtenidas por el método de raspado: a) *M. flavida* con cuerpos de sílice en forma de silla de montar constreñidos en la parte media, b) *M. breviseta* con cuerpos de sílice equidimensionales en forma de silla de montar formando una doble equis, c) *M. nigra* con cuerpos de sílice solitarios entre dos células largas y d) *M. aguascalientensis* con cuerpos de sílice y de corcho en pares, (cch) células de corcho, (cs) células de sílice.

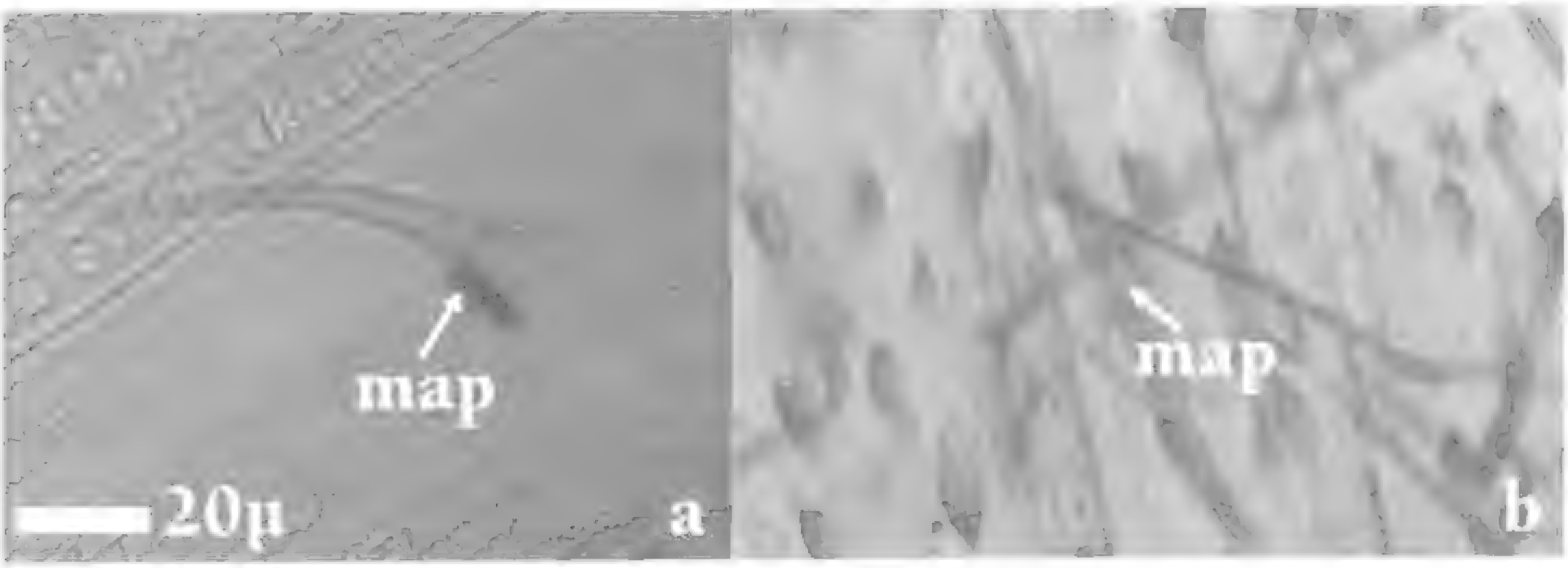

Fig. 7. Macropelos, obtenidos por el método de raspado: a) *M. tenella*, macropelos escasos y de consistencia rígida, b) *M. pubescens*, con abundantes macropelos largos y suaves.

Agua Caliente de los baños El Encanto, *L.M. Villarreal 7114* (SLPM); Santa Ana Tepetitlán, Zapopan, *Díaz Luna 3746* (GUADA). Nayarit: Barranca 0.5 km al S de Santa Teresa del Nayar, mpio. El Nayar, *Díaz Luna 9556* (GUADA). Sinaloa: between La Fraguita and El Madroño, carr. Durango-Mazatlán, mpio. Concordia, *Beetle M-3730* (ENCB).

M. annua. Durango: 14 km al NNE de San José de Avino, mpio. Pánuco de Coronado, ***R. Serrano s.n.*** **(INEGI).**

M. appressa. Baja California: 1.5–2.5 mi upstream from Rincón, 4.5 mi NE of Sta. Catarina, 64 mi SE of Ensenada, *R.E. Brother 708* (MEXU); 10.5 km W of La Rumorosa along hwy 2, mpio. Tecate, ***Thorne 60422*** **(MEXU).**

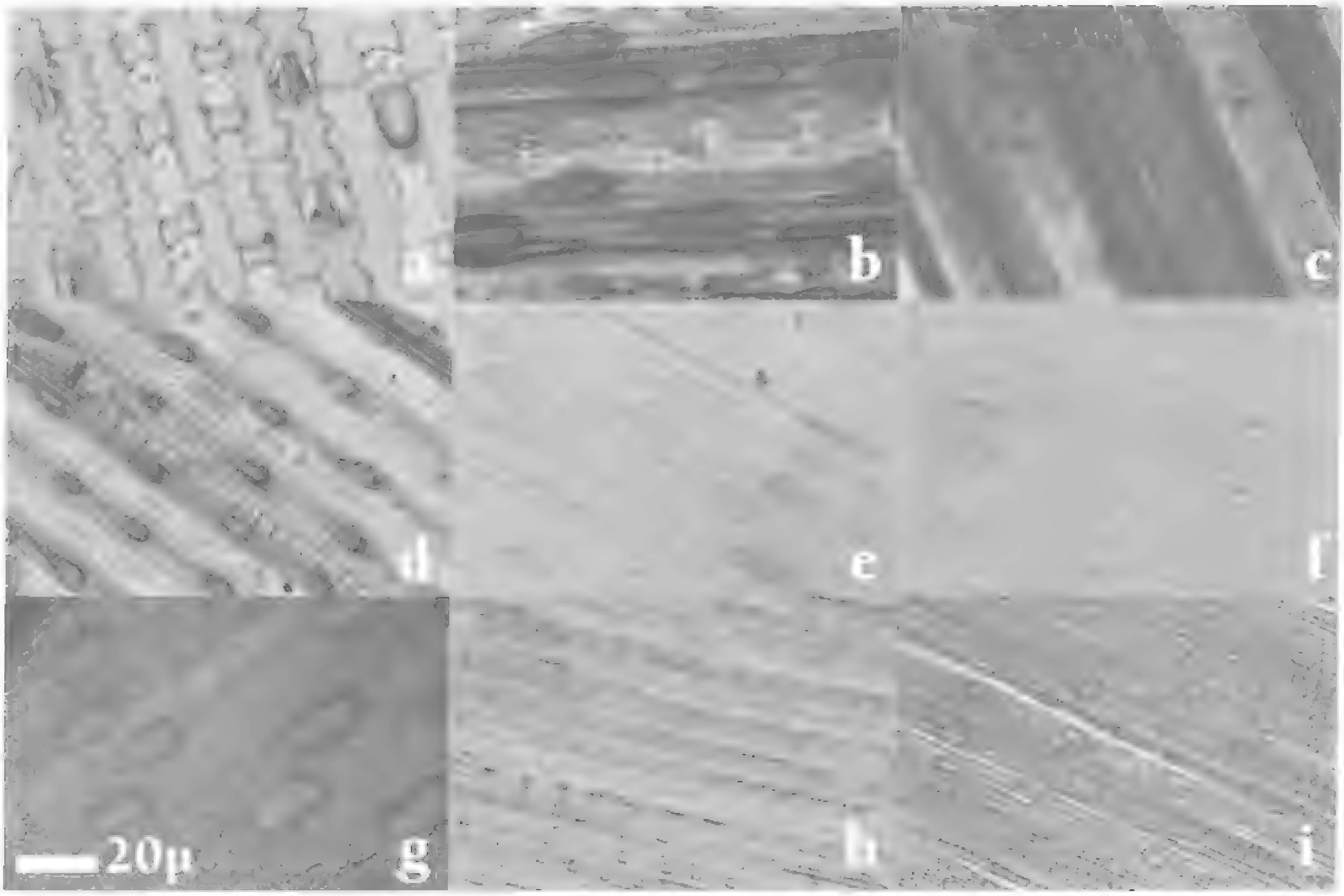

Fig. 8. Especies del género *Muhlenbergia* en el grupo IA: a) *M. aguascalientensis*, b) *M. rigens*, c) *M. palmeri*, d) *M. pauciflora*, e) *M. capillaris*, f) *M. dubia*, g) *M. glabrata*, h) *M. rigida*, i) *M. laxiflora*. Nótese 1 sola hilera de estomas en la zona intercostal, aguijones en la zona costal y ausencia de papilas.

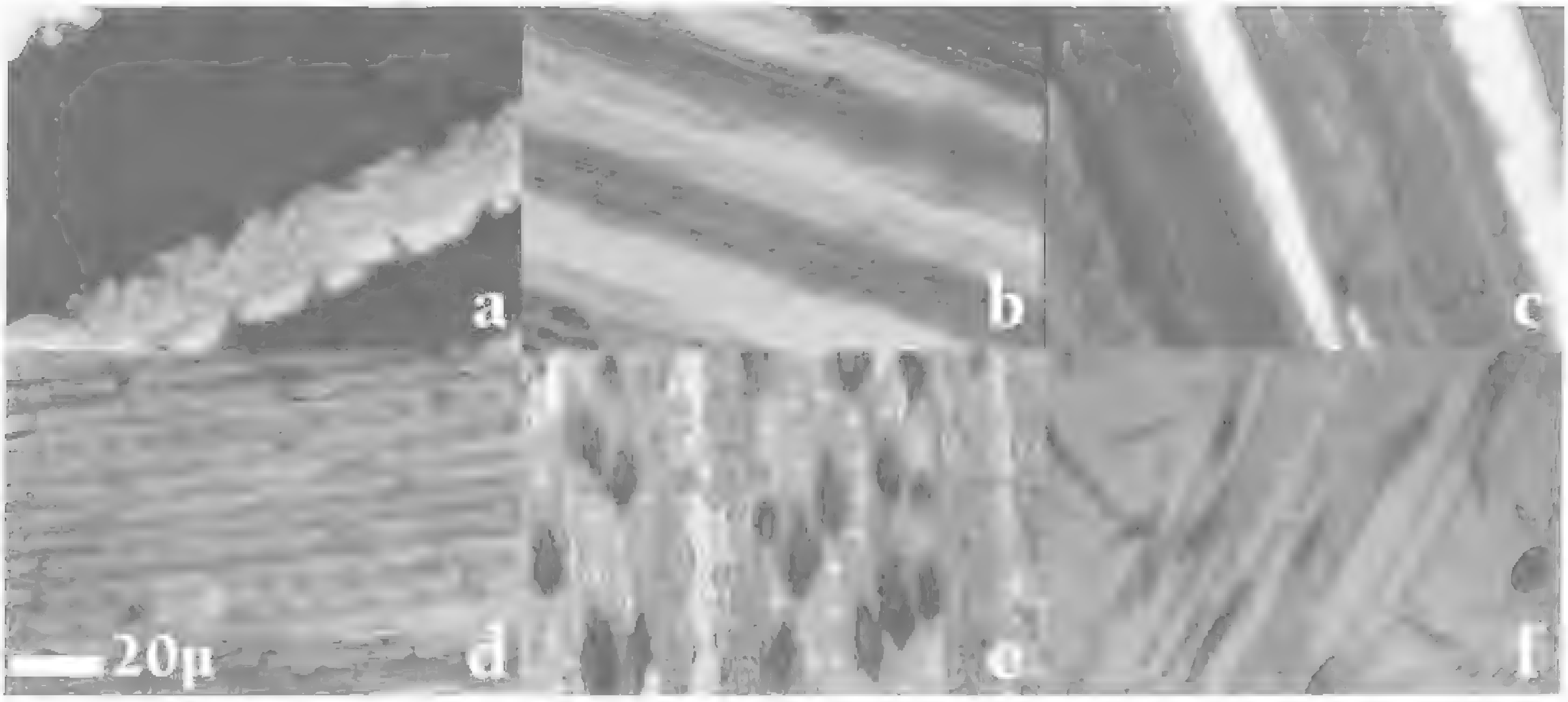

Fig. 9. Especies representativas de *Muhlenbergia* en el grupo IB: a) *M. distichophylla*, b) *M. emersleyi*, c) *M. gooddingii*, d) *M. grandis*, e) *M. robusta*, f) *M. xanthodas*. Nótese 2 hileras de estomas en la zona intercostal, aguijones en la zona costal y ausencia de papilas.

M. atenacea. Coahuila: Cañón de la Vaca, sierra Santa Fé del Pino, mpio. Ocampo, ***J. Passini 5248* (ENCB).** Nuevo León: 2 km SSW Puerto Grande en el camino a Castillo, mpio. Galeana, *H. López s.n.* (INEGI).

M. arenicola. Aburto Chihuahua: 15 mi W of Jiménez, mpio. López, *Reeder & C. Reeder 4875* (ENCB). Durango: 9 mi N of Zacatecas state line along hwy 49, mpio. Sta. Clara, *Reeder & C. Reeder 6475* (ENCB). Nuevo León: 4 km al E

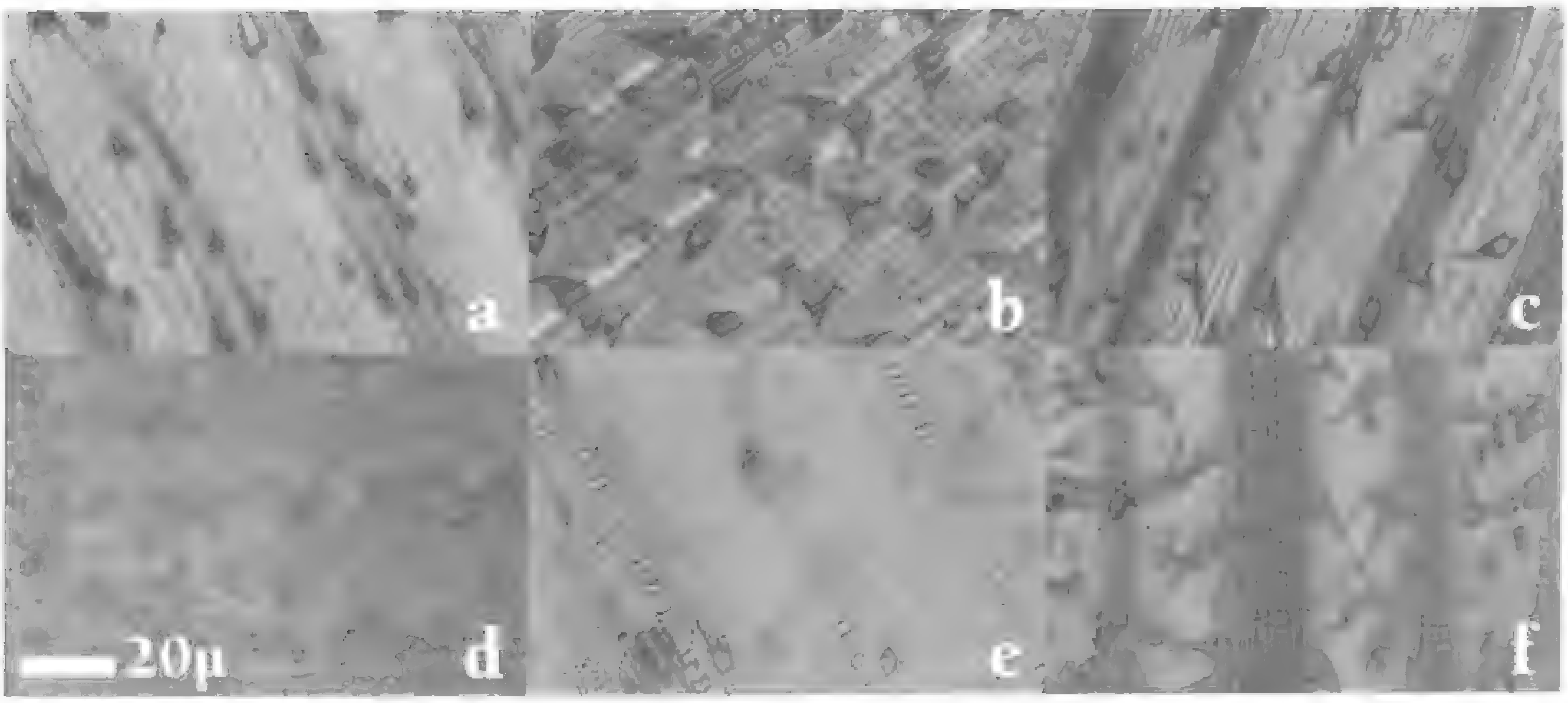

Fig. 10. Especies representativas del grupo IIA: a) *M. appressa*, b) *M. microsperma*, c) *M. parviglumis*, d) *M. schreberi*, e) *M. polycaulis*, f) *M. brevifolia*. Nótese la presencia de papilas, aguijones y celulas largas con paredes anticlinales onduladas, por lo general sin sinuosidades.

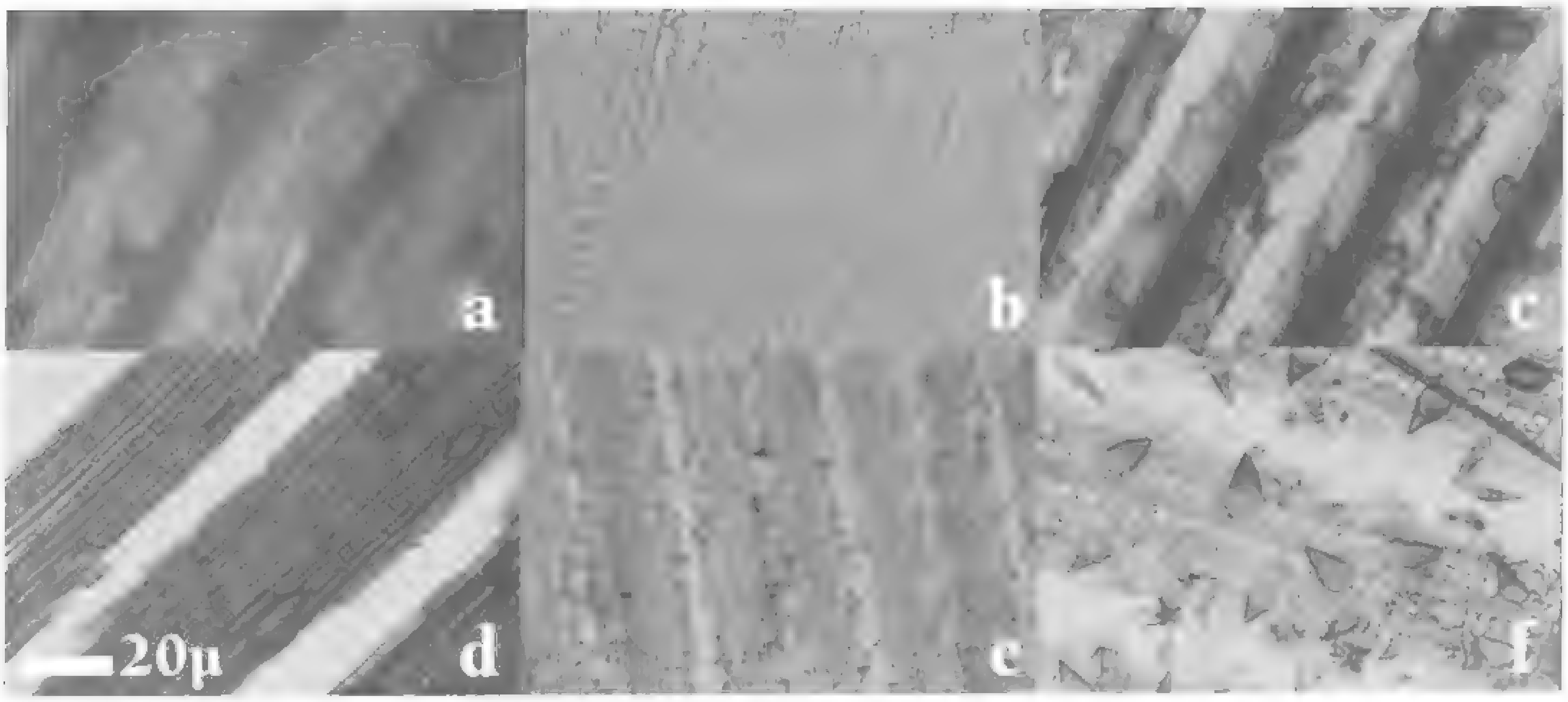

Fig. 11. Especies del grupo IIB: a) *M. pubigluma*, b) *M. brevis*, c) *M. glauca*, d) *M. virescens*, e) *M. dumosa*, f) *M. watsoniana*. Nótese la presencia de papilas, aguijones y celulas largas con paredes anticlinales por lo general sinuosas en forma de U y de V.

del ejido María de Ramos, mpio. Galeana, *L. Ledesma s.n.* (INEGI). San Luis Potosí: Estación Berrendo, mpio. Charcas, *Rzed 6575* (SLPM).

M. argentea. Chihuahua: 15.3 mi S of Mex 127 and 6.9 mi NE of la Bufa, mpio. Guachochi, *P.M. Peterson, Annable & Y. Herrera 971* (CIIDIR).

M. arizonica. Chihuahua: Chihuahua-Sonora border, Rancho Carretas, mpio. Janos, *L.H. Harvey 1624* (TAES); Rocky hills near Chihuahua, *Pringle 402* (ENCB). Durango: about 41 mi N of Cd. Durango, mpio. Canatlán, ***Reeder & C. Reeder 6482* (ENCB).**

M. arsenei. Baja California: E of Upper Vallecitos Meadow, Sierra San Pedro Mártir, mpio. Mexicali, ***Moran 23729* (ENCB);** cerca Observatorio Astronómico Nacional, sierra San Pedro Martir, mpio. Ensenada, *F. Takaki s.n.* (INEGI).

M. articulata. Aguascalientes: Milpillas de Arriba, mpio. Jesús María, *Zúñiga 204* (MEXU); Arroyo El Terrero, mpio. Calvillo, *Zúñiga 236* (MEXU). Hidalgo: 20 km al SSE de Ixmiquilpan, mpio. Progreso de Obregón, *L. González 3116* (ENCB); Los Tepetates, 4 km al W de Sta. Ma. Amajac, mpio. Atotonilco el Grande, *J. García 139* (MEXU). Jalisco: km 219 de la carr. México-Nuevo Laredo entre Zimapán y Jacala, mpio. Zimapán, *R. Cruz 1417* (ENCB). Querétaro: 1 km al S de Vizarrón, mpio. Cadereyta de Montes, *Mora*

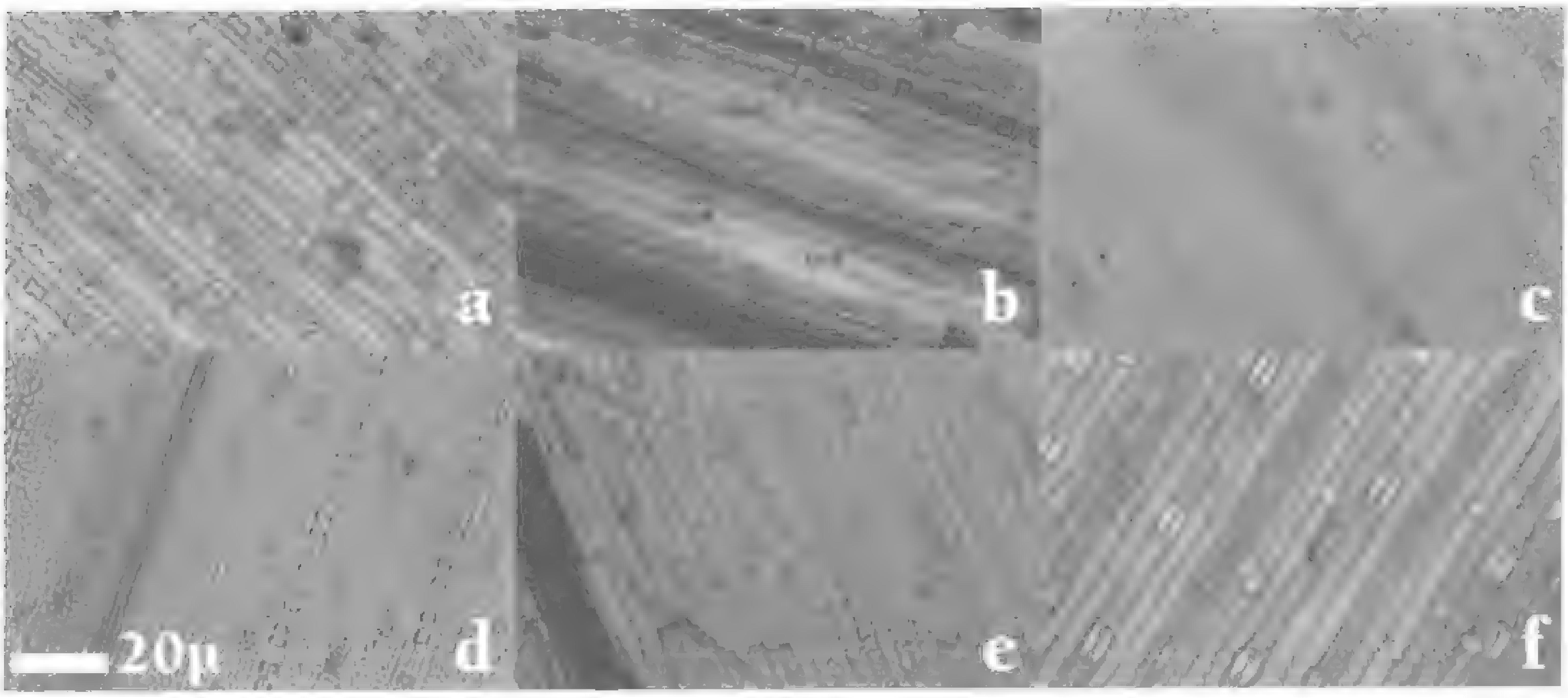

Fig. 12. Especies del grupo IIIA: a) *M. annua*, b) *M. implicata*, c) *M. minutissima*, d) *M. strictior*, e) *M. texana*, f) *M. fragilis*. Nótese la ausencia de papilas y de aguijones.

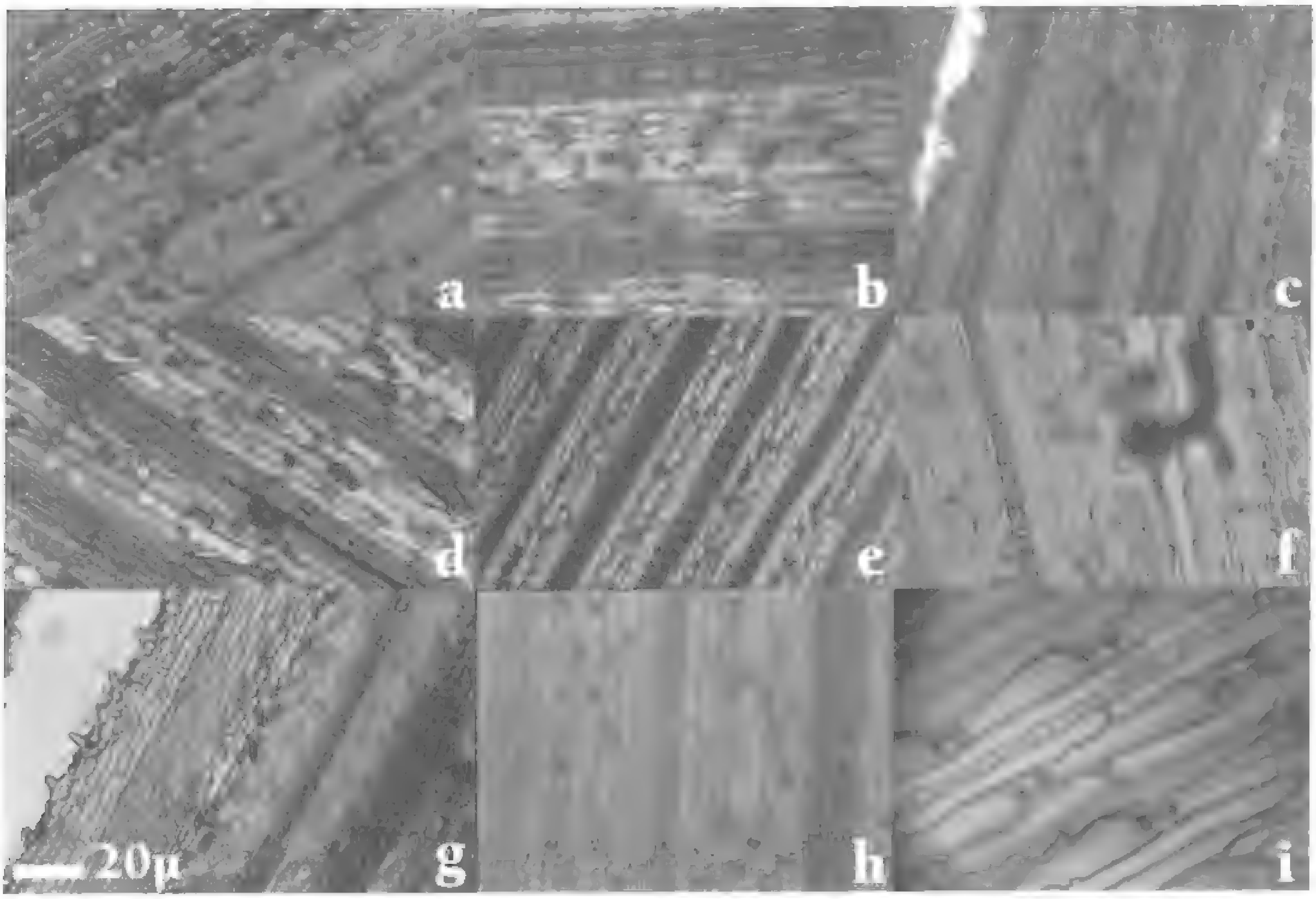

Fig. 13. Especies incluidas en el grupo IIIB: a) *M. depauperata*, b) *M. plumbea*, c) *M. repens*, d) *M. arsenei*, e) *M. asperifolia*, f) *M. arizonica*, g) *M. vaginata*, h) *M. utilis*, i) *M. majalcensis*. Nótese la presencia de papilas y la ausencia de aguijones.

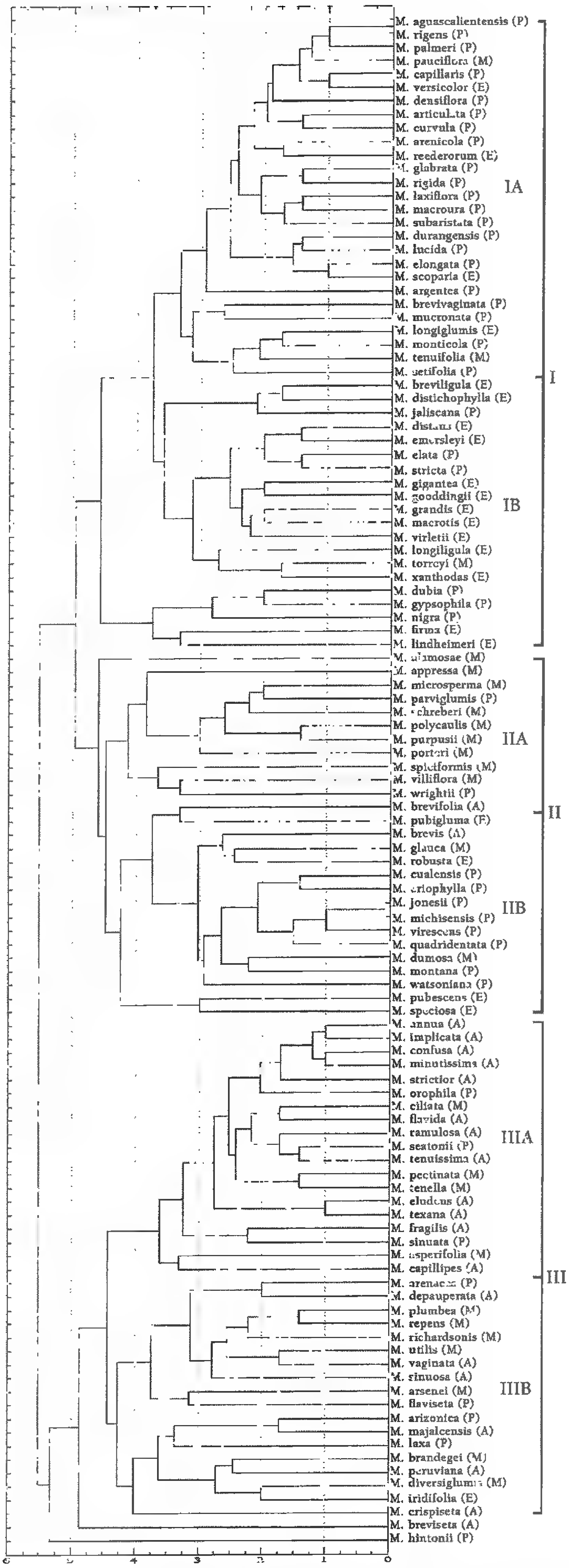

Fig. 14. Dendrograma agrupando 113 especies del género *Muhlenbergia* revisadas en este estudio.

Benítez 353-AMB (MEXU). San Luis Potosí: 10 km al W de Guadalcázar, *Rzed. 4930* (ENCB); 3 km al SW de Guadalcázar, *Rzed. 6809* (TAES).

M. asperifolia. Baja California: Sierra San Pedro Martir, mpio. Mexicali, *R. Morán 17973* (TAES). Chihuahua: about 9 mi N of Las Delicias, ***Reeder & C. Reeder 2615*** **(ENCB).** Coahuila: Ferriño's laguna area, mpio. Cuatrociénegas, *D. Pinkava & E. Lehto & D. Keil 5409* (ENCB).

M. brandegei. Baja California Sur: aprox. 25 km S of La Paz, W side of Isla La Partida, mpio. La Paz, *P.M. Peterson & Annable 4760* (US).

M. brevifolia. Jalisco: Ejido El Zapote, mpio. Pénjamo, ***Mora Benítez 251-AMB*** **(MEXU).**

M. breviligula. Chiapas: 3 mi S of Aguacatenango along road to Pinola Las Rosas, *Breedlove & Raven 13135* (TAES); near Venustiano Carranza along the road to pugiltic, *Laughlin 2702* (TAES).

M. brevis. Chihuahua: 0.7 mi W of Nuevo Majalca, 8.5 mi W of hwy 45, ***P.M. Peterson & Annable 4512*** **(ENCB);** 15.6 mi NE of El Vergel on hwy 24, mpio. Balleza, *Peterson & Annable 4061* (US). Durango: 5.4 mi W of Navíos, 42 mi W of Durango on hwy 40, *Peterson & Annable 4586* (US).

M. breviseta. Jalisco: about 12 mi E of Zacapú on road from Guadalajara to Morelia, ***Reeder & C. Reeder 1447*** **(ENCB).** Michoacán: Cerros Las Viudas y Las Flores, al SE del Rancho Seco, *A. Martínez 871* (ENCB).

M. brevivaginata. Aguascalientes: Laguna Seca, mpio. San José de Gracia, *Y. Herrera & O. Rosales 604* (UAA). Durango: Potrero Las Escobas, San Juan de Michis, mpio. Súchil, *J. Alvarado 725* (CHAPA). Zacatecas: km 30 de la terracería entre Tlaltengo y Jalapa, mpio. Tlaltenango de Sánchez Román, *Balleza 2720* (ENCB).

M. capillaris. Jalisco: Las Popas de Arriba, 14 km al S de Ojuelos, *Santana-Michel 1501* (ENCB). Oaxaca: 4 km al S de Ejido Benemérito de las Americas, camino a Flor de Cacao, *E. Martínez 10785* (MEXU). Querétaro: 3 km al S de San Joaquín, mpio. San Joaquín, ***R. Fernández 3248*** **(ENCB).**

M. capillipes. Chihuahua: Rancho Teseachic, mpio. Namiquipa, *Beetle M-3266* (MEXU); 22 mi SE of Chuichupa on the road to Madera, mpio. Madera, *Reeder & C. Reeder 2673* (US); 24 mi SW of La Junta on road to Creel, mpio. Guerrero, *Y. Herrera 953* (ENCB); 0.5 mi W of Flores Magón, mpio. Buenaventura, *Reeder, Reeder & Soderstrom 3496* (US).

M. ciliata. Jalisco: km 29 por la carr. Zapopan-San Cristóbal de la Barranca, *Santana-Michel 1973* (IBUG); parte más alta del Cerro Grande de Cujaruato, al SW de la Piedad, *Rzed. & McVaugh 515* (ENCB). Michoacán: Cerro Colorado, mpio. Pátzcuaro, ***J.M. Escobedo 240-A*** **(ENCB);** 7 km al E de Villa Jiménez, sobre el camino a Copándaro, *Rzed. 40757* (ENCB).

M. confusa. México: Terrenos de Juchitepec, mpio. Juchitepec, O. Domínguez (MEXU).

M. crispiseta. Durango: 6 mi W of Río Chico crossing W of Cd. Durango, *Reeder & C. Reeder 4645* (CHAPA); Camino los Herreras-Topia km 64, mpio. Santiago Papasquiaro, *M. González-Elizondo 3252-a* (CHAPA).

M. cualensis. Jalisco: Minas Zimapán, por la brecha a Cuale, *R. Guzmán 6100* (MEXU); Minas Zimapán, por la brecha a Cuale, *Santana-Michel* 1217 (SLPM); El Caracol, 1 km al W de la Mina de Zimapán, *González.-Villareal 3283* (ENCB).

M. curvula. Guanajuato: 6 mi NE of Guanajuato, *Rzed. 16133* (UAA); 6 km al NE de Santa Rosa, sobre el camino a Dolores Hidalgo, *Rzed. 42071* (CHAPA). San Luis Potosí: Sierra de San Miguelito, 30 km al WSW de San Luis Potosí, carr. a Villa de Arriaga, *Rzed. 29381* (CHAPA). Zacatecas: aprox. 38 km al W de Jalpa sobre la carr. a Tlaltenango, 30 km del entronque con la carr. Jalpa-Juchipila, *Rzed. & McVaugh 974* (ENCB).

M. densiflora. Chiapas: about 15 mi SE of Teopisca, *Reeder & C. Reeder 2045* (ENCB).

M. depauperata. Chihuahua: just N of Villa Matamoros on hwy 45 towards Parral, *P.M. Peterson & Annable 4579* (US). Hidalgo: about 8 mi S of Ixmiquilpan, mpio. Chilcuautla, *Reeder & C. Reeder 1611* (CHAPA). Jalisco: 1 km al N de Ventura, mpio. Villa Hidalgo, ***Rzed. 11455*** **(TAES).**

M. distans. Aguascalientes: El Zapote, 1 km al S de Cosío, *de la Cerda 4194* (UAA). D.F.: base de la Sierra de Sta. Catarina, al N de Tlatelolco, Delegación Tláhuac, *Rzed. 37470* (SLPM). Jalisco: Sierra de Cuale, entre Cuale y Talpa, mpio. Talpa de Allende, *J.V. de la Torre 8634* (ENCB). México: Sierra de Guadalupe, base del cerro Tontepec al SW de Coacalco, mpio. Coacalco de Berriozabal, *Rzed. 38248* (TAES).

M. distichophylla. Jalisco: SSE of Puerto Vallarta, 14 km from the opening of the Zimapán Mine, 1 km W of Providencia boundary El Tuito-El Cuale, *Santana-Michel 2348* (ENCB); nacimiento del Río Salado, aprox. 30 km al W de Guadalajara, ***Rzed. 15490*** **(ENCB).**

M. diversiglumis. Durango: Canelas, 1 km por el camino a Durango, *M. González-Elizondo 274-a* (ENCB). Michoacán: 4 km al S de Jesús del Monte sobre el camino a San Miguel, mpio. Morelia, *Rzed. 41323* (UAA).

M. dubia. Aguascalientes: Bajío La Canoa, Sierra San Blas de Pabellón, mpio. San José de Gracia, *de la Cerda 4085* (UAA). Coahuila: 153.2 km NW of Múzquiz on hwy 53 towards Boquilla del Carmen, *P.M. Peterson & Annable 10594* (US). Guanajuato: Rancho de Enmedio, Sierra Sta. Rosa, ***Y. Herrera & Cortés 1421*** **(UAA).** Jalisco: 25 km al NW de Bolaños por la brecha a Los Asmoles, mpio. Bolaños, *Santana-Michel 1766* (IBUG). San Luis Potosí: Sierra La Viga, mpio. Arteaga, *C.E. Zermeño 1155* (INEGI).

M. dumosa. Colima: Yerbabuena, mpio. Comala, *M. Navarrete 596* (MEXU). Michoacán: about 25 km S of Arteaga, road to Playa Azul, mpio. Lázaro Cárdenas, ***Díaz Luna 9300*** **(GUADA).** Zacatecas: Florencia, 3 km al W del pueblo, mpio. Benito Juárez, *Díaz Luna 15291* (GUADA).

M. durangensis. Durango: 33 km de La Guajolota, por el camino a Platanitos, mpio. Mezquital, *M. González-Elizondo 1692* (US); bajada del camino a San Fco. de Lajas, mpio. Pueblo Nuevo, *S. González 2324* (ENCB). Jalisco: km 22.5 brecha Bolaños-Tenzompa, mpio. Mezquitic, *Ramírez & Guzmán 641* (IBUG).

M. elata. 2 km al E de El Limón, mpio. Santa Ma. del Oro, M.J. Sepúlveda 987 (CIIDIR).

M. elongata. Chihuahua: Cañón del 54, mpio. Chihuahua, *J.M. Peña s.n.* (ENCB); 12 mi S of Villa Matamoros on hwy 45

towards Parral, *Reeder & C. Reeder 4886* (ENCB); Batopilas, mpio. Batopilas, *R. Fierros 1663* (MEXU).

M. eludens. Chihuahua: hills near Chihuahua, *Pringle 3052, 3056* (TAES); El Tigre to El Rancho de Robles, NE Sonora, mpio. Bavispe, *J. Vera 1957* (CHAPA); Tomochi, 2 km alrededor del poblado, mpio. Guerrero, *M. Vergara 153* (MEXU).

M. emersleyi. Jalisco: 7 mi SSW of Mazamitla, ***Reeder & C. Reeder 6329* (ENCB).** Durango: 4 km al W de La Parrilla, mpio. Nombre de Dios, *S. Acevedo & S. González 2779* (ENCB). Querétaro: Puerto de Los Velázquez, mpio. Pinal de Amoles, *V. Jaramillo, G. Villegas & A. Miranda 808* (MEXU).

M. eriophylla. Aguascalientes: lado SW de presa La Araña, mpio. San José de Gracia, *G. García 1371* (UAA). Guanajuato: 12 km al NE de Tierras Negras, mpio. Pénjamo, *Rzed. 51290* (CIIDIR). Durango: Cerro Blanco, Reserva de la Biosfera "La Michilía", mpio. Súchil, *M. González-Elizondo 3740* (CIIDIR). Michoacán: Cerro de Ucareo, mpio. Zinapécuaro, *L. Oseguera 52* (MEXU).

M. firma. Chiapas: about 15 mi SE of Teopisca, mpio. Teopisca, *Reeder & C. Reeder 2045* (ENCB). Guanajuato: 53 km al E de San Luis de la Paz, sobre carr. a Xichú, mpio. Victoria, *Rzed. 41390* (CIIDIR). México: 6 km de Tlazala de Fabela por la carr. a Nicolás Romero, mpio. Isidro Fabela, *M. González-Ledezma, J. García & I. Hernández 108* (SLPM).

M. flavida. Chihuahua: 15.3 mi S of Mex 127 and 6.9 mi NE of la Bufa, mpio. Guachochi, ***M.E. Sequeiros 1647* (UAA);** Sierra Milpillas 28.1 mi E of Los Tanques on road to Chinipas, 1.6 mi N of Los Chinipas, *P.M. Peterson & Annable 4174* (MEXU). Sonora: 4 km W de El Talayote, 35 km E de Yécora, mpio. Yécora, *P. Tenorio 4520* (ENCB).

M. flaviseta. Chihuahua: Parque Nacional de Cascada Basaseachic, 1 km airline S of Cascada, mpio. Ocampo, *M. Vergara 139* (MEXU). Durango: Predios del ejido La Victoria, mpio. Pueblo Nuevo, ***D. Aceval 696* (MEXU);** Potrero Chaides, 9 km al NE de La Mesa, brecha a El Yaqui, mpio. Tepehuanes, *P. Tenorio & C. Romero 2080* (MEXU).

M. fragilis. Guanajuato: Rancho Rinconcillo de los Remedios, mpio. Comonfort, *J.J. Macías 591* (MEXU). Guerrero: 18 km al NW de Chilpancingo, mpio. Chilpancingo de los Bravo, *O. Tellez 4552* (MEXU). Sonora: N of Cananea, Ejido José María Morelos, ***Beetle M-7867* (ENCB).** Zacatecas: al W de Pueblo Viejo, sierra de Morones, cerro de Piñones, ladera E, mpio. Juchipila, *Balleza & Adame 9193* (SLPM).

M. gigantea. Chiapas: Kulaktik, mpio. Tenejapa, *A.S. Ton 4570* (ENCB); 12 km S of Mexican hwy 190 near Rizo de Oro, mpio. Cintalapa, *Breedlove 20641* (TAES). Durango: orillas del pueblo de Topia, rumbo a Cuevecillas, *A. Benítez 1105* (CHAP). Jalisco: km 217 carr. Guadalajara-Barra de Navidad, mpio. Cihuatlán, *L.M. Villareal 8303* (IBUG). Michoacán: 5 km al N Tlalpujahua, mpio. Tlalpujahua, 16-Dic.-1986, *Rzed. 42265* (ENCB).

M. glabrata. Michoacán: 9 mi W of Zacapú, mpio. Zacapú, *Reeder & C. Reeder 4746* (MEXU). San Luis Potosí: 5 km E Soledad de Zaragoza, mpio. Xilitla, ***Rzed. 7122* (ENCB);** Sierra de Monte Grande, arroyo de Carbonerías, al NW del cerro de Juan Chepe, mpio. Charcas, *J.A. Reyes 375* (CHAPA).

M. glauca. Aguascalientes: Bajío La Canoa, Sierra San Blas de Pabellón, mpio. San José de Gracia, ***de la Cerda 4090* (UAA).** Coahuila: Sierra de Zapalinamé, 5 km S Saltillo in San Lorenzo Canyon, mpio. Saltillo, *Hatch, Morden & J. Valdés 4498* (MEXU). Durango: 15 mi W of El Pino, 29 mi W of Durango, *Reeder & C. Reeder 3127* (ENCB). San Luis Potosí: 12 km W Estación Berrendo, mpio. Charcas, *Rzed. 6576* (CHAPA); Sierra de Monte Grande, Tanque de adentro, mpio. Charcas, *J.A. Reyes 579* (CHAPA); 3 mi SW of San Luis Potosi, *Pringlei 1893* (TAES); km 30 carr. San Luis Potosí-Ojuelos, 3 km entronque a la Amapola, mpio. Villa de Arriaga, *A. Romero s.n.* (SLPM).

M. gooddingii. Sonora: 19 km al W de Yécora, ***Beetle M-6169* (MEXU);** S of Ures, mpio Ures, *Tañori 8310* (MEXU); El Cañón de la Bellota, Sierra de la Cabellera, mpio. Agua Prieta, *J. Vera 2110* (US).

M. grandis. Guanajuato: 9 km WNW de la Valenciana, mpio. Guanajuato, ***Rzed. 49767* (CIIDIR).** Jalisco: ca 13 mi NNE of Guadalajara, mpio. Zapopan, *Reeder & C. Reeder 4724* (US); cerca de El Corte Colorado, La Resolana, *Rezedowski 15037* (ENCB).

M. gypsophila. Nuevo León: Municipality Galeana, *O. Domínguez 1000, 1254* (MEXU); *D. Fuentes s.n.* (ENCB); La Joya, Cuesta Blanca, 15 km de Aramberri rumbo a Zaragoza, mpio. Zaragoza, *J. Valdés VR-2554* (ENCB); 2 km al S del Salero, mpio. Galeana, ***Valdés & Marroquín 1619* (ENCB).** San Luis Potosí: 12 mi NW of Matehuala on road to Cedral, *Reeder & C. Reeder 4812* (ENCB).

M. hintonii. México: alrededores del Llano de la Horca, mpio. Tlalmanalco, *Rzed. 31662* (SLPM).

M. implicata. Aguascalientes: Barranca El Temascal, mpio. Calvillo, ***L. Juárez 987* (UAA).** Chihuahua: 0.7 mi W of Nuevo Majalca, 8.5 mi W of hwy 45, *P.M. Peterson & Annable 4514* (TAES); La Joya, Cuesta Blanca, 15 km de Aramberri rumbo a Zaragoza, mpio. Zaragoza, *J. Valdés VR-2554* (ENCB). México: Temascaltepec, mpio. Temascaltepec, *Hinton 2079* (ENCB). *14.8 mi NE of El Vergel, mpio. Balleza, P.M. Peterson & Annable 4079 (TAES).* Michoacán: 15 mi W of Jiquilpan, mpio. Jiquilpan, *Reeder & C. Reeder 6326* (ENCB).

M. iridifolia. Jalisco: 15 km S Talpa, sobre camino a La Cuesta, mpio. Talpa de Allende, *Rzed. 15235* (ENCB).

M. jaliscana. Jalisco: camino Sta. Rosa, 1 km antes del Salvador, mpio. Tequila, *A. Navarro 213* (IBUG); San Cristóbal, mpio. Zapopan, *A. Navarro & E. Cervantes 158* (IBUG).

M. jonesii. California: 9.5 mi SE of hwy 97 on Military Pass Rd., NE side of Mt Shasta, *P.M. Peterson & Annable 4857* (US).

M. laxa. Veracruz: Cerro Macuiltepec, just outside Jalapa, mpio. Xalapa, *Reeder & C. Reeder 5991* (ENCB); Cerro Macuiltepec, mpio. Xalapa, *V. Hernández 80* (MEXU).

M. laxiflora. Durango: about 3 mi E of El Salto, mpio Pueblo Nuevo, ***Reeder & C. Reeder 2559* (ENCB).** Oaxaca: 34 mi NW of Oaxaca, mpio. Oaxaca, *Reeder & C. Reeder 2188* (MEXU).

M. lindheimeri. Coahuila: 4 mi WSW of Nava, *Reeder & C. Reeder 4814* (ENCB).

M. longiglumis. Guanajuato: 28 km NNW Juventino Rosas sobre carr. a Guanajuato, *Rzed. 41197* (CHAPA). Jalisco: Guadalajara, mpio. Guadalajara, *Pringle 2365* (US); Ayo El Grande, mpio. Jesús María, *A. Navarro 781* (MEXU).

M. longiligula. Chihuahua: about 15 mi S of Madera, mpio. Madera, *Reeder & C. Reeder 2639* (ENCB). Sonora: N of Cananea, Ejido José María Morelos, *Beetle M-7823* (MEXU).

M. lucida. Chihuahua: 10.7 mi S of Mexico 127 on road to Batopilas, *Y. Herrera, P.M. Peterson & Annable 946* (CIIDIR); 78 km de la Junta de Basaseachic, mpio. Guerrero, *R. Fierros 1691* (MEXU).

M. macrotis. Aguascalientes: Barranca Río Gil, mpio. Calvillo, *de la Cerda. 4409* (UAA); Barranca El Empinado, mpio. San José de Gracia, d*e la Cerda 3943* (UAA). Jalisco: 3 km al E de la Estación Biológica Las Joyas, camino al cerro Almela, mpio. Autlán, *E.J. Jodziewcz & T.S. Cochrane 4818* (IBUG).

M. macroura. Aguascalientes: Bajío La Canoa, Sierra San Blas de Pabellón, mpio. San José de Gracia, *de la Cerda 4103* (UAA). Puebla: Campo experimental San Juan Tetla, vertiente E del Ixtaccihuatl, mpio. San Martín Texmelucan, *A. May Nah 971* (ENCB).

M. majalcensis. Chihuahua: 20 mi W of México 45 and about ½ mi E of Cumbres de Majalaca, mpio. Riva Palacio, ***P.M. Peterson, Annable & Y. Herrera 949* (CIIDIR).**

M. michisensis. Durango: Potrero Las Escobas, San Juan de Michis, mpio. Súchil, *J. Alvarado 723* (CHAPA).

M. microsperma. Michoacán: 51 km de Pátzcuaro rumbo a Uruapan, mpio. Ziracuaretiro, *A. Díaz Osorno 358* (ENCB); Cañada del río Grande, cerca de Cointzio, mpio. Morelia, ***Rzed. 45281* (CIIDIR).** Oaxaca: 6 km al E de Guadalupe Cuautepec, mpio. Santiago Miltepec, *A. Salinas & A. Campos 3690* (MEXU). San Luis Potosí: Rancho El Palmar, potrero Tortugas, mpio. San Luis Potosí, *I.V. Rivas & M. González-Ledezma 226* (SLPM).

M. minutissima. Chihuahua: Cabecera de la cañada de Recogoata, mpio. Bocoyna, *B. Tah 44* (MEXU). Tamaulipas: km 26 carr. Victoria-San Luis Potosí, mpio. Victoria, *G. Villegas 169* (MEXU). Tlaxcala: camino de San Cosme Xalostoc a Terrenate, 5.5 km de la carr. Apizaco-Huamantla, ***H. Vibrans 2835B* (CHAPA).**

M. montana. Aguascalientes: La Ciénega, mpio. San José de Gracia, d*e la Cerda 3989* (UAA). Chihuahua: carr. San Juanito-La Junta, 17 km, mpio. Guerrero, *B. Tah 8* (MEXU); Chihuahua-Sonora border, Rancho Carretas, mpio. Janos, *Harvey 1639* (ENCB); 12 mi SW of Chuhichupa, mpio. Madera, *Spellenberg & Zimmerman 8951* (ENCB). Durango: 15 km al W de Canatlán, sobre Mesa de Aguirre, *J. Blando s.n.* (ENCB). Oaxaca: 2 km al E de San Antonio Abad, mpio. Concepción Buenavista, *R. Cruz 2322* (ENCB).

M. monticola. Coahuila: 25 km S of Saltillo at the rancho Recreacion El Chorro, mpio. Saltillo, *Hatch, Morden & Valdés 4590* (TAES); 5 km S of Saltillo, in San Lorenzo Canyon, mpio. Saltillo, *Hatch, Morden & Valdés 4495* (TAES).

M. mucronata. Durango: 7.3 mi N of Charcos on road towards San Juan de Michis, mpio. Mezquital, *P.M. Peterson, S. González & Knowles 13646* (US).

M. nigra. México: Paso de Cortés, entre Popocatepetl e Iztaccihuatl, mpio. Amecameca, ***A. Cortés s.n.* (INEGI);** Parque Nacional Nevado de Toluca, mpio. Texcaltitlán, *Beaman 1708* (ENCB).

M. orophyila. México: Paso de Cortés, 13 km al E de Amecameca, mpio. San Nicolás de los Ranchos, *Koch 76266* (CHAPA).

M. palmeri. Chihuahua: Sierra Madre Occidental, along río Corareachi, ***P.M. Peterson & Catalán 17605* (CIIDIR);** Parque Natural Barranca del Cobre, 1.6 km E of La Bufa, mpio. Guachochi, *P.M. Peterson & Knowles 13579* (US).

M. parviglumis. Hidalgo: Zempoala, mpio. Zempoala, ***A. Ventura 1495* (ENCB).**

M. pauciflora. Sonora: E of Cananea, Sierra de los Ajos, mpio. Frontera, ***Beetle M-7869* (ENCB).**

M. pectinata. Guerrero: 24.5 mi N of Taxco on hwy 55, mpio. Pilcaya, ***P.M. Peterson & Annable 4666* (ENCB).**

M. peruviana. Aguascalientes: El Pandito de Vázquez, Sierra de San Blas Pabellón, mpio. San José de Gracia, ***G. García 2335* (UAA).** México: 2.3 mi E of hwy 3 on road to Nevado de Toluca, mpio. Zinacantepec, *P.M. Peterson & Annable 4636* (TAES); 6 mi W of pass on road from Toluca to Temascaltepec, mpio. Zinacantepec, *Dunn 17197* (ENCB). Michoacán: 9.3 mi E of Opopeo on hwy 41, mpio. Salvador Escalante, *P.M. Peterson & Annable 4622* (ENCB).

M. plumbea. D.F.: Cuilotepec, Sierra de Ajusco, deleg. Tlalpan, *E. Manrique 1144* (MEXU). Hidalgo: Laguna de Apan, mpio. Apan, ***R. Cruz 411* (ENCB).** Tlaxcala: Camino de San Cosme Xalostoc a Terrenate, 5.5 km de la carr. Apizaco-Huamantla, *H. Vibrans 2836* (ENCB).

M. polycaulis. Aguascalientes: Barranca El Empinado, mpio. San José de Gracia, ***de la Cerda 3943* (UAA).** Chihuahua: 6 mi E of Buenaventura, *Reeder & C. Reeder 3200* (ENCB). Sonora: El Cañón de la Bellota, Sierra de la Cabellera, mpio. Agua Prieta, *J. Vera 2097* (TAES). Zacatecas: brecha Jeréz-Guadalupe Victoria, mpio. Jerez, Balleza 2222 (CHAPA).

M. porteri. Durango: 3.5 km al ESE de El Carmen, carr. 45 a Durango, *J. Blando s.n.* (INEGI). San Luis Potosí: km 428 carr. Central, mpio. San Luis Potosí, *A. Gómez 925* (SLPM). Sonora: Río de Bavispe NE Sonora, La Mesa de Las Carreras, W of Colonia Morelos, *J. Vera 2054* (US).

M. pubescens. Aguascalientes: camino a presa de La Araña, mpio. San José de Gracia, *G. García s.n.* (UAA); 8 km al SW de la hacienda El Garabato, mpio. Jesús María, d*e la Cerda 3486* (UAA). Durango: 10 km al SW de Súchil, carr. en construcción a Tepic, mpio. Súchil, ***S. González & Y. Herrera 1512* (CIIDIR).** San Luis Potosí: La Amapola, ejido El Pachón, mpio. San Luis Potosí, *A. Avila 37* (SLPM).

M. pubigluma. Coahuila: Rancho Demostrativo "Los Angeles" 48 km al S de Saltillo, ***J.A. Villarreal & J. Valdés 3370* (ENCB).**

M. purpusii. San Luis Potosí: Entronque a San Agustín, mpio. Matehuala, *S. Villegas y E. García s.n.* (TAES); San José del Refugio, km 550 carr. central entre el entronque y Matehuala, *F. Medellín 1130* (SLPM).

M. quadridentata. México: 10 km al E de Amecameca, sobre el camino a Tlamacas, *Koch 76269* (TAES). Michoacán: parte alta del cerro del Burro, mpio. Huiramba, ***Rzed. 44627* (UAA).** Veracruz: Vidal Díaz Muñóz, mpio. Perote, *G. Hernández 314* (INEGI).

M. racemosa. Coahuila: Serranías del Burro, rancho El Bonito, 12 km N of headquarters, mpio. Acuña, *J. Valdés & D. Riskind VR-1277* (TAES).

M. ramulosa. Baja California: E of Upper Vallecitos Meadow, Sierra San Pedro Mártir, mpio. Mexicali, *M. del Real 300* (MEXU). Chihuahua: km 85 carr. Balleza-Guachochi, mpio. Guachochi, *M.E. Siqueiros 1606* (MEXU); 12 mi NW of Madera, mpio. Madera, *Reeder & C. Reeder 2649* (SLPM). Jalisco: 1 km al SW de la comunidad Maquixtla, mpio. Zacatlán, *S. Aguirre S-189* (MEXU). México: Volcán de Toluca, mpio. Toluca, *R. Sohns & E. Matuda 1006* (TAES); camino viejo al CICITEC, límites Milpa Alta y Juchitepec, *A. Miranda, G. Villegas & R. Méndez 890* (MEXU). Michoacán: alrededor de Jeráhuaro, mpio. Zinapécuaro, *Rzed. 46165* (MEXU).

M. reederorum. Durango: Ejido Echeverria de la Sierra, mpio. Durango, *J.A. Ochoa & R. Martínez 315* (MEXU),

M. repens. Aguascalientes: La Ciénega, mpio. San José de Gracia, ***de la Cerda 3981* (UAA).** Jalisco: La Tapona, mpio. Tula, *M.H. Cervera 132* (MEXU). San Luis Potosí: Cerro San Pedro, mpio. San Luis Potosí, *M.H. Castro 84* (MEXU).

M. richardsonis. Baja California: Sierra San Pedro Martir, Los Llanitos, mpio. Mexicali, *Moran 28016* (US).

M. rigens. Aguascalientes: Camino cerro del Tepozán (orilla de arroyo), mpio. Calvillo, *G. García 286* (UAA); Puentes Cuates, mpio. Calvillo, de *la Cerda 9398* (UAA). Durango: W de Sta María de Ocotán, mpio. Mezquital, ***M. González-Elizondo y S. Acevedo 1554* (CIIDIR).**

M. rigida. Aguascalientes: 3 km al W de La Estancia, mpio. San José de Gracia, ***G. García 1867* (UAA).** Chiapas: about 2 mi SE of San Cristóbal de las Casas, *Breedlove & G. Davidse 54703* (SLPM). Durango: aprox. 18 km al E de Durango, carr. a México, serranías frente a la fábrica de celulosa, *Gould & J. Morrow 7916* (TAES). Jalisco: 15 km al SW de Matanzas, mpio. Ojuelos, *Díaz Luna 4412* (GUADA); 2 mi NW of Tequila at the edge of the Barranca Country, mpio. Tequila, *Cervantes y Castro 19* (MEXU). Michoacán: alrededores de los filtros viejos, cerca de Morelia, *A. Miranda, G. Villegas & R. Méndez 20* (MEXU). Tlaxcala: Hacienda San Francisco, cerca de Hermenegildo Galeana, mpio. Huamantla, *A. Rodríguez 669* (MEXU).

M. robusta. Durango: km 60 carr. Durango-Mazatlán, mpio. Durango, *Beetle M-7745* (MEXU). Guanajuato: 2 km al NW de La Gavia, sobre el camino a Cortazar, mpio. Cortazar, *Rzed. 40924* (SLPM). México: parte alta de la Sierra de Alcaparrosa, mpio. Tepotzotlán, *Rzed. 29939* (SLPM). Puebla: carr. San Fco. Totimehuacán a Santo Tomás Chiautla, mpio. Puebla, *S. Aguirre S-140* (MEXU). San Luis Potosí: Cerro El Chiquihuitero, cerca de Tortugas de Arriba, mpio. Santa María del Río, ***F. Tataki 1984* (UAA).** Zacatecas: 3 km al E de Maravillas, mpio. Villanueva, *Ma.C. Arteaga 722* (MEXU).

M. scoparia. Jalisco: Arroyo Agua Caliente de los baños El Encanto desviación a Pajaritos, Zapopan, *L.M. Villareal 7317* (IBUG); El Tuito, mpio. Cabo Corrientes, *M. del C. Mendoza s.n.* (IBUG). Michoacán: El Cerrito, 1.5 km E Jeráhuaro, mpio. Zinapécuaro, *M.J. Jasso 1709* (CIIDIR).

M. schreberi. Tamaulipas: La Begonia, 2 km al S de San José, mpio. San Carlos, ***Briones 1306* (SLPM).**

M. seatonii. México: alrededor de Peñas Largas, mpio. Epazoyucan, *Rzed. 38485* (CIIDIR)

M. setifolia. Coahuila: 26 mi NW of Rancho Margareta, 90 mi NW of Sabinas, mpio. Múzquiz, *Gould 10688* (TAES).

M. sinuosa. Sonora: E of Cananea, Sierra de los Ajos, mpio. Frontera, *Beetle M-7875, M-7876* (TAES).

M. speciosa. Jalisco: 4–5 km SE de Platanarillos, 11–12 km al ESE de Minatitlán, *R. Cuevas & L. Guzmán 1182* (IBUG). Sinaloa: 24.4 mi NW of Surutato, 12 mi SW of Los Hornos, mpio. Badiraguato, *Breedlove 16816* (TAES).

M. spiciformis. Chiapas: 3 mi S of La Trinitaria, mpio. La Trinitaria, *P.H. Raven 13235* (TAES). Querétaro: 2 km de Pinal de Amoles carr. a Jalpan, mpio. Pinal de Amoles, *L.G. Rincón 206* (MEXU).

M. stricta. Durango: about 3 mi E of El Salto, mpio Pueblo Nuevo, *Reeder & C. Reeder 2551* (SLPM). Jalisco: 5 km al W de Xalisco, *J. Sepúlveda 846* (MEXU); La Primavera, en la Arena, mpio. Zapopan, *R. González 87* (MEXU). Zacatecas: 24 km SE of Durango state line on hwy 49, then 3 km to NE, E of Estación Microondas Morelos, mpio. Juan Aldama, *R. Spellenberg & M. Mahrt 10725* (CIIDIR).

M. strictior. Chihuahua: Cusarare, S of Creel, mpio. Guachochi, *R.A. Bye 5191* (MEXU); Parque Nacional de Cascada Basaseachic, 1 km airline S of Cascada, mpio. Ocampo, *Torres 3777* (MEXU). Durango: about 9 mi E of El Salto, mpio. Pueblo Nuevo, ***Reeder & C. Reeder 4676* (ENCB).**

M. subaristata. Durango: km 95 carr. Durango-Mazatlán, a 5 km del Salto, mpio. Pueblo Nuevo, *Miranda 1382* (MEXU); km 109 carr. Durango-Mazatlán, mpio. Pueblo Nuevo, *Beetle M-7735* (MEXU).

M. tenella. Jalisco: Barranca El Huizichi, mpio. Tolimán, *Díaz Luna 20145* (GUADA). México: 1.75 km al NE de Nesón Nuevo, mpio. Tejupilco, *A. Ramírez 595* (MEXU). Nayarit: alrededores de Tepic, *F. Rodríguez 001* (MEXU). Veracruz: Tío Linga, mpio. Soledad de Doblado, ***A. Carrillo 236* (MEXU);** El Aguacero en el río La Venta, mpio. Ocozocuautla, *E. Martínez 22006* (MEXU).

M. tenuifolia. Aguascalientes: 2 km al E de Tepezalá, mpio. Tepezalá, *de la Cerda 3894* (UAA); Puentes Cuates, mpio. Calvillo, de *la Cerda 4394* (UAA); W de la estación de microondas, mpio. Rincón de Romos, ***O. Rosales 418* (UAA).** Guanajuato: Rancho Divino Rostro, km 21 carr. Dolores Hidalgo-San Luis Potosí, mpio. Dolores Hidalgo, *S. Rojas 174-SRV* (MEXU). Querétaro: 1 km al S de Vizarrón, mpio. Cadereyta de Montes, *Zamudio 3356* (UAA).

M. tenuísima. Jalisco: aprox. 45 km al E de El Aserradero, sobre el camino a Manuel M. Diéguez, *L.M. Villareal 5870* (IBUG). Nayarit: alrededores de Tepic, *Beetle, G. Harding y R. Guzmán M-6293* (MEXU).

M. texana. Chihuahua: 22 km al S de Humira, 21.8 km al SW de la dev. a La Bufa, mpio. Batopilas, *R. Torres 3690* (MEXU); Sierra Milpillas, 24.1 mi E of Los Tanques on road to Milpillas, mpio. Chinipas, ***Beetle, R. Alcaráz & R. Cuadra 9203* (MEXU).** Nayarit: Puente de Comatlán, mpio. La Yesca, *A. Castro 081* (MEXU).

M. torreyi. Sonora: N of Cananea, Ejido José María Morelos, *Beetle M-7866* (TAES). San Luis Potosí: Ejido Vicente Guerrero, mpio. Charcas, *H. Bravo 0003* (MEXU).

M. utilis. Chihuahua: Mesa de El Poleo, ejido El Largo, mpio.

Madera, *Blanco 08/77* (IBUG). Guanajuato: Rancho El Molino, mpio. Dolores Hidalgo, *R. Santillán 673* (MEXU). Hidalgo: Pachuca, mpio. Pachuca de Soto, *R. Guzmán 3786* (MEXU). México: 1.25 km al SE de San Diego Linares, mpio. Toluca, *A. Ramírez 497* (MEXU). San Luis Potosí: Ejido Cerrito Blanco, 10 km E Matehuala, ***A. Bolaños 203* (MEXU).**

M. vaginata. Colima: Sierra de Halo, near a lumber road leaving the Colima hwy 7 mi SSW of Tecalitlán and SE to San Isidro, *Koch, J. Villa & J. Chávez 267* (SLPM). D.F.: Caldera El Guarda, al S de Parres, deleg. Tlalpan, *A. Miranda y P. Guerrero 101* (MEXU). Durango: km 115 carr. Durango-Mazatlán, mpio. Pueblo Nuevo, *R. Rangel 410* (MEXU). Jalisco: 1–2 mi E of Tapalpa, *Santana-Michel 1441* (IBUG). México: San Miguel, mpio. Temascaltepec, *E. Manrique, Jaramillo & Núñez 393* (MEXU). Sinaloa: between Mazatlán and Durango, between La Fraguita and El Madroño, Durango-Mazatlán, mpio Concordia, ***Beetle M-3718* (MEXU).**

M. versicolor. Chiapas: at Escopetazo, mpio. Ixtapa, *Breedlove & G. Davidse 53960* (SLPM). Guerrero: Amojileca, mpio. Chilpancingo, *U. González 1963* (MEXU). Puebla: carr. San Alejo-Coatepec, desv. a Reynoso, 300 m terracería adentro, mpio. Coatepec, *R. Méndez 1268* (MEXU); 14.2 km sobre la carr. a Coyomeapan, *L. Aragón 508* (MEXU). Oaxaca: Tlacolula, mpio. Tlacolula de Matamoros, *L. García 5* (MEXU); Rancho Teja, 5 km W of Ixtlán de Juárez, *B. Benz & K. Benz 694* (IBUG).

M. villiflora. Nuevo León: La Cardona, mpio. Bustamante, *R. López & A. Brito 042a* (MEXU); Ejido El Jarro, 14 km del poblado Dr. Arroyo carr. a Matehuala, *J. Garza & M. Castillo 192* (MEXU). San Luis Potosí: km 195 carr. Querétaro-San Luis Potosí, mpio. Soledad de Graciano Sánchez, *M.A. Reyes 64* (MEXU). Zacatecas: Palula, mpio. Villa de Cos, *E. Manrique, Beetle & G. Harding 1285* (MEXU).

M. virescens. Guanajuato: 6 mi NE of Guanajuato, ***Reeder & C. Reeder 4750* (ENCB);** 21 km al W de Dolores Hidalgo, sobre la carr. a Guanajuato, *Rzed. 41131* (IBUG). Michoacán: 19 km al E de Queréndaro, sobre la carr. a Maravatío, mpio. Queréndaro, *Rzed. 40988* (SLPM).

M. virletii. México: Terrenos de Juchitepec, mpio. Juchitepec, *A. Ventura 818* (MEXU); Pedregal de Huisihuilango, mpio. Juchitepec, *A. Ventura 1132* (MEXU); al N de Jilotepec, mpio. Jilotepec, *V. Jaramillo, G. Villegas & A. Miranda 901* (MEXU).

M. watsoniana. Jalisco: Meza de León en el predio de La Primavera, mpio. Zapopan, ***L.M. Villareal 13196* (IBUG);** Cerro El Huiluxtle, mpio. Zapopan, *L.M. Villarreal & Pérez de la Rosa 2893B* (IBUG). San Luis Potosí: cerro near San Luis, *Schaffner 1067* (US).

M. wrightii. Baja California: Yerba Buena, mpio. Ensenada, *Moran & Thorne 14236* (TAES). Chihuahua: 13 mi W of Cuahutémoc on hwy 16, mpio. Cuahutémoc, *P.M. Peterson 9586* (US).

M. xanthodas. Chiapas: 18 km al NE de Tuxtla Gutiérrez rumbo al Cañón del Sumidero, ***A.J. Zenón 0043* (MEXU).**

AGRADECIMIENTOS

Se reconoce y agradece el financiamiento recibido de la Comisión Nacional para el Uso y Manejo de la Biodiversidad (CONABIO-V024), y del Instituto Politécnico Nacional (SIP-20010344). A las autoridades del CIIDIR IPN Unidad Durango, les agradecemos el facilitar la tarea que nos permitió llevar a cabo y concluir el presente estudio. A los curadores de los herbarios consultados, se les agradece sus atenciones. Se agradecen las observaciones de 3 revisores anónimos y del Dr. Lipscomb, que ayudaron a mejorar el presente trabajo sustancialmente. En el presente reporte se vierten resultados parciales, generados durante el desarrollo del proyecto "Biosistemática del género *Muhlenbergia* de México" SIP-20010344.

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PRIMER REPORTE DE *CYSTOPTERIS REEVESIANA* (ASPLENIACEAE) PARA MÉXICO

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RESUMEN

Se cita como primer vez a *Cystopteris reevesiana* Lellinger para México. La distribución previamente conocida de la especie es del suroeste de los Estados Unidos de América, encontrándose en este trabajo que también se ha colectado de tres estados del noroeste de México.

ABSTRACT

Cystopteris reevesiana Lellinger is reported for the first time as occurring in Mexico. The species is known from the southwestern U.S.A., but also has been collected in the northwestern Mexico.

Durante la colecta de material botánico en el sur de Chihuahua, llamó la atención la presencia de un *Cystopteris* diferente al *C. fragilis* (L.) Bernh., que por ser el mas frecuente, es el mejor conocido. Después de ubicarlo taxonómicamente se encontró que es *C. reevesiana* Lellinger. Al parecer, es el primer reporte en el que se da a conocer la presencia de la especie en Chihuahua.

Especimen de respaldo (voucher): **MÉXICO. Chihuahua. Municipio de Guadalupe y Calvo:** Cerro El Mohinora, 25° 57'39.14" N, 107° 02'21.59" W, 3142 m, 1 Oct 2007, *C. Flores López 439, 460* (ANSM).

La especie crece en un bosque de oyamel con *Pseudotsuga menziesii, Abies durangensis, Picea mexicana, Pinus arizonica, Salix paradoxa, Ribes madrensis, Senecio toluccanus* y *Erigeron fraternus*. Es poco común en el área y forma colonias esparcidas en lugares con humedad. *Cystopteris reevesiana* fue descrito en 1981. Forma parte del complejo de especies relacionadas con C. fragilis. Se caracteriza por presentar frondas 2–3 pinnadas, con segmentos muy angostos, escamas del rizoma de color café claro y carencia de pelos glandulares en el estipite.

Cystopteris reevesiana es conocido de Arizona, Colorado, Nuevo México, Utah y de Trans-Pecos en Texas, pero no había sido reportado de Chihuahua en México (Knobloch y Correll 1962; Mickel y Smith 2004). Sin embargo al investigar si la especie no era conocida de México, encontramos que en algunos herbarios existen colectas de Sonora (TEX, UC), de Baja California (UC) e incluso de Chihuahua (UC), por lo que la especie extiende su distribución conocida del suroeste de los Estados Unidos al noroeste de México.

AGRADECIMIENTOS

Agradecemos la ayuda de los doctores J.T. Mickel y A. R. Smith en la identificación del material botánico y proporcionar información sobre la especie. A Remedios Aguilar por la revisión del escrito.

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BOOK NOTICE

William Hawthorne and Ntim Gyakari. 2006. **Photoguide for the forest trees of Ghana: a tree-spotter's field guide for identifying the largest trees.** (ISBN 0-85074-164-5, pbk.). Oxford Forestry Institute, Department of Plant Sciences, South Parks Road, Oxford OX13RB, United Kingdom. (**Orders:** www.nhbs.com, +44 (0)1803 865913, +44 (0)1803 865280 fax). $30.00, 432 pp., color photos, b&w figures, 5 3/4" × 7 1/4".

From the publisher: "A field guide to the larger trees that occur in Ghanaian forests. It is based on photographs and drawings and is designed to minimize the need for reading complicated botanical text. This guide includes 326 species, virtually all Ghana's forest canopy and emergent trees. The photos show leaves, fruit, flowers, bark, wood and trunk and any other identification aids. Each species account has brief notes on ecology, size, bark & slash, leaves, flowers, fruits, and similar species. Similar species are mentioned and distinguished."

Line drawings of botanical terminology are included on the inside front and back covers of this book. A common name index, scientific name index, and ruler are also included. The front cover of the book boasts a grid of tiny color photographs, the very same bark, leaf, and twig pictures from the species descriptions. But take a step back from this cover and you'll see that the smaller images have been arranged such that they resemble from afar a big eye—presumably the watchful, curious orb of the Ghanaian "tree-spotter."

J. Bot. Res. Inst. Texas 3(1): 308. 2009

FLORISTIC COMPOSITION, ABUNDANCE, AND DISTRIBUTION PATTERN OF WOODY PLANTS IN A TROPICAL SAVANNA IN NORTHERN GHANA

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ABSTRACT

The floristic composition, abundance and distribution pattern of woody plants in a tropical savanna in the Sinsabligbini Forest Reserve in northern Ghana was studied using 15 circular vegetation plots of 10 m radius. In total, 2534 individuals of woody plants belonging to 62 species in 19 families were identified. The most species rich and abundant families were Fabacaeae, Combretaceae and Rubiaceae. The abundant woody plants included *Dichrostachys cinerea* (L.) Wright & Arn. (Fabaceae), *Pteleopsis suberosa* Engl. & Diel. (Combretaceae), *Combretum collinum* Fresen. (Combretaceae), *Dalbergia afzeliana* G. Don. (Fabaceae) and *Terminalia mollis* Laws. (Combretaceae). The majority (80.6%) of the woody plant species were found to be highly aggregated in their pattern of distribution while twelve species showed some degree of randomness. The study has shown that the floristic composition and abundance of plants is very variable in different areas of the Guinea Savanna Zone.

Key Words: Woody plants; Guinea savanna; Singsaglebini Forest Reserve; Ghana

RESUMEN

La composición florística, abundancia y patrón de distribución de plantas leñosas en una sabana tropical en la Sinsabligbini Forest Reserve en el norte de Ghana se estudió usando 15 parcelas de vegetación circulares de 10 m de radio. En total se identificaron 2534 individuos de plantas leñosas pertenecientes a 62 especies de 19 familias. Las familias con mayor número de especies y abundantes fueron Fabacaeae, Combretaceae y Rubiaceae. Las plantas leñosas abundantes incluyen *Dichrostachys cinerea* (L.) Wright & Arn. (Fabaceae), *Pteleopsis suberosa* Engl. & Diel. (Combretaceae), *Combretum collinum* Fresen. (Combretaceae), *Dalbergia afzeliana* G. Don. (Fabaceae) y *Terminalia mollis* Laws. (Combretaceae). De la mayoría de las especies leñosas (80.6%) se encontró que estaban altamente agregadas en su patrón de distribución mientras que doce especies mostraron algún grado de azar. El estudio ha mostrado que la composición florística y abundancia de plantas es muy variable en diferentes áreas de la zona de sabana de Guinea.

INTRODUCTION

The most extensive vegetation type in Ghana is the guinea savanna. It is estimated to cover about 60.77% of the total land-mass of Ghana (Anonymous 2002). Previous publications of studies on the guinea savanna vegetation in Ghana include that of Vigne (1936), Taylor (1952), Baker (1962), Lawson et al., (1969), Houssain and Hall (1969), Hopkins (1979), Oteng-Yeboah (1996) and recently Asase and Oteng-Yeboah (2007). Other studies have examined the effect of fire on the savanna (Ramsay & Rose Innes 1963; Brookman-Amissah et al. 1980). Despite these contributions, few studies have documented the diversity and abundance of species of plants found in different areas in the savanna zone of Ghana. This current documentation is of management importance as it contributes to a better understanding of the need to conserve and sustainably utilize plant diversity.

The Sinsabligbini Forest Reserve in northern Ghana is one of the important protected areas in the savanna zone of Ghana. The reserve was created in 1956 to protect the headwaters of Moya River and its tributaries. To the best of our knowledge, however, there is no published information on the different species of plants found in the reserve that could assist those involved in the management of the reserve to develop appropriate management strategies for the conservation of the vegetation in the reserve.

The objective of the present study was therefore to (i) document the floristic composition, abundance and distribution pattern of woody plants in the Sinsabligbini Forest Reserve in northern Ghana and (ii) compare it with other areas in the Guinea Savanna Zone of West Africa particularly Ghana. It is hoped that this information could assist in the development of strategic management plans for the reserve.

MATERIALS AND METHODS

Study area

The study area at the Sinsabligbini Forest Reserve is situated about 20 km from Tamale, the Northern Regional Capital of Ghana. The reserve is located between latitude 09° 24 138 N and longitude 00° 38 377 W, and covers an area of 72.72 km^2. About 0.2 km^2 of the reserve area has been converted into a plantation of *Eucalytptus* sp., *Tectona grandis* L. and *Anogeissus leiocarpus* Guill & Perr. The natural vegetation in the reserve area is guinea savanna. The terrain is generally flat and the soil in most areas of the reserve is shallow with exposed laterite. In seasonally flooded areas of the reserve the soil is mainly made up of clay and silts.

The reserve area experiences one rainy season between May and October each year with a peak period in August and a dry season from November to March. The average annual rainfall and temperature are 1034.1 mm and 26.7° C, respectively. There are over 10 communities living around the reserve and the people are mostly from the Dagomba ethnic group. Most of the people living around the reserve are farmers.

Methods

The woody plants in the natural vegetation area of the reserve were studied using vegetation plots. With reference to Landsat EM 2000 satellite images and topographical maps, we located different habitat areas in the reserve and randomly demarcated circular vegetation plots of 10 m radius (ca. 314 m^2 size) in each of the habitat areas. In total, 15 vegetation plots were examined; at least three plots were demarcated for each different habitat area. All species of woody plants found rooted within each plot were identified and their individual plants counted.

The identification of the species of plants encountered was later confirmed using relevant literature (Arbonnier 2000; Hutchinson & Dalziel 1957–1972), and by comparison with already identified specimens at the Ghana Herbarium located at the Department of Botany, University of Ghana.

Data analysis

The individual-based rarefaction methodology described by Gotelli and Colwell (2001) was used to estimate the expected number of species for the construction of species accumulation curve with 95% confidence interval. The free statistical software Estimates version 8.0 (Gotelli 2006) was used for the species accumulation curve. The program was set to randomized samples with replacement and shuffle; the individual of plants among plots within species 1000 times.

The variance: mean ratio of individuals per unit area can be used as a measure of the degree of randomness or aggregation in populations or whole communities (Pilou 1977; Sokal & Rolf 1981). Chi-squared test was used to determine whether the pattern of distribution was significantly random or aggregated based on the variance: mean ratio calculated for each species (Lambshead & Hodda 1994; Rice & Lambshead 1994).

RESULTS

Floristic composition

In total, 2534 individuals of woody plants belonging to 62 species in 48 genera and 19 families were identified in the reserve. The individual-based species accumulation curve shows that the majority of woody plants in the reserve were sampled during the study as seen in the curve as it reaches the asymptote (Fig. 1). The list of species, their families and growth-forms are presented in Table 1. The majority (40.3%) of the species were big trees, followed by small trees (29.0%) and shrubs (27.4%). Two species namely, *Dalbergia afzeliana* G. Don. and *Opilia celtidifolia* Endl. ex Walp.were the only lianas identified. About 62.9% of the woody plant genera in the reserve consisted of only one species. Genera with two or more species were *Acacia* (3 species), *Annona* (2 species), *Bridelia* (2 species), *Combretum* (4 species), *Gardenia* (2 species), *Lannea* (2 species), *Strychnos* (2 species), *Terminalia* (3 species) and *Vitex* (2 species).

The most species rich family (29%) was Fabacaeae, followed by Combretaceae (14.5%), and Rubiaceae (11.3%). Other taxonomic families with many species were Verbenaceae (6.5%), Euphorbiaceae (6.5%), Anac-

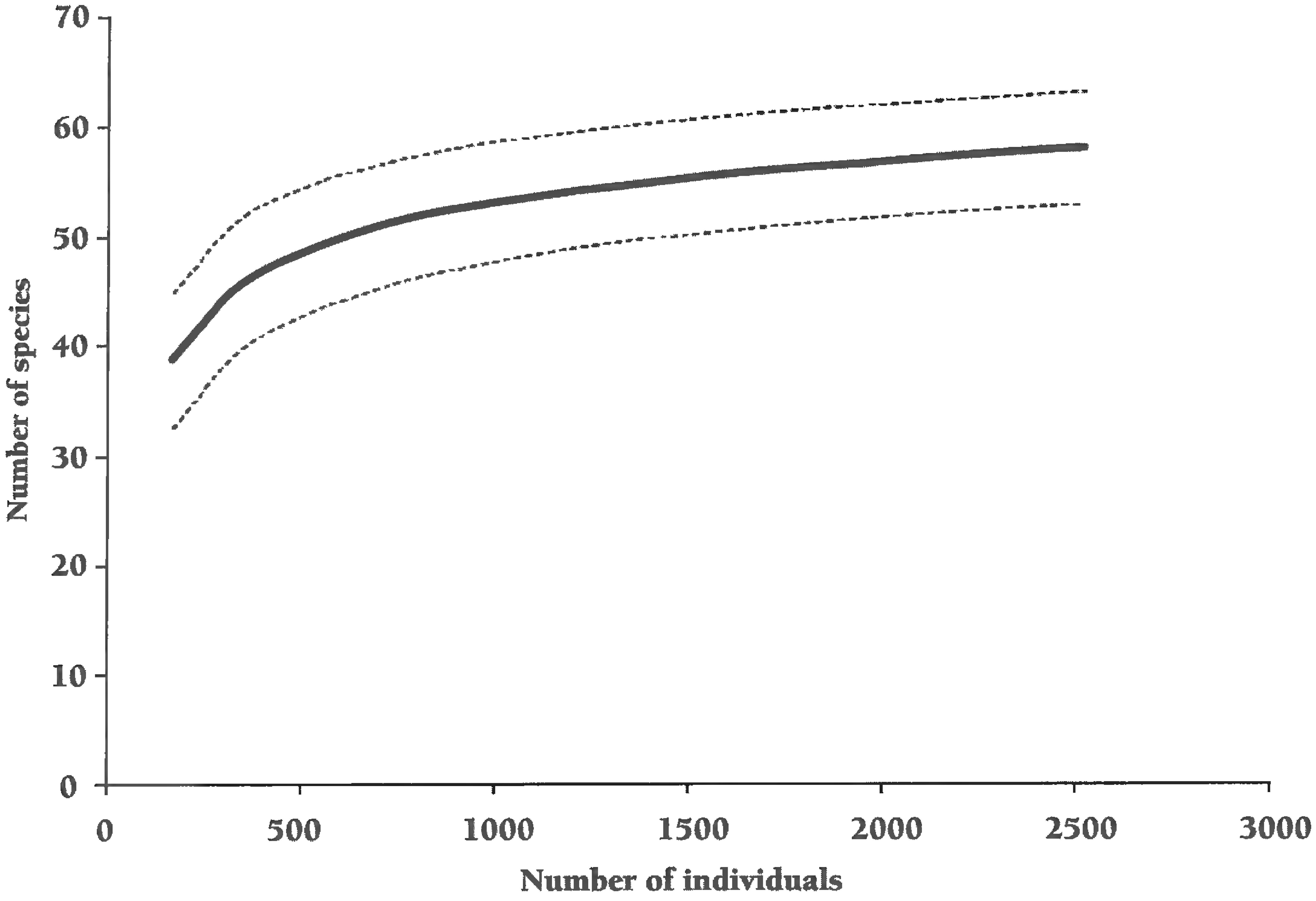

Fig. 1. Individual-based species accumulation curve for woody plants in Singsaglebini Forest Reserve in northern Ghana.

ardiaceae (4.8%) and Annonaceae (4.8%) in decreasing order of number of species (Table 2). Ten (52.6%) of the families, namely, Bignoniaceae (*Stereospermum kunthianum* Cham.), Bombacaceae (*Bombax costatum* Pellegr. & Vuillet), Celastraceae (*Maytenus senegalensis* (Lam.) Exell), Cornaraceae (*Rourea coccinea* (Schumach. & Thonn.) Hook.f., Moraceae (*Ficus* sp.), Opiliaceae (*Opilia celtidifolia* Endl. ex. Walp.), Polygalaceae (*Securidaca longepedunculata* Fresen.), Proteaceae (*Protea madiensis* Oliv.), Sapotaceae (*Vitellaria paradoxa* C.F. Gaertn.) and Tiliaceae (*Grewia venusta* Fresen.) were each represented by only one species indicated in brackets. The families with highest number of individuals were Fabaceae and Combretaceae. These families contributed about 68.7% of individuals to the woody flora in the reserve. Seven other families (Bombacaceae, Celastraceae, Moraceae, Opiliaceae, Polygalaceae, Proteaceae and Verbanaceae) contributed less than one percent of the total number of individuals per family. The families Moraceae and Polygalaceae were least abundant with each one represented by only one individual plant recorded in the reserve.

Abundance and distribution pattern

The six most abundant woody plants in the reserve were *Dichrostachys cinerea* (L.) Wight & Arn. (Fabaceae), *Pteleopsis suberosa* Engl. & Diels (Combretaceae), *Combretum collinum* Fresen. (Combretaceae), *Dalbergia afzeliana* G. Don. (Fabaceae), *Terminalia mollis* S.Vidal. (Combretaceae), and *Vitellaria paradoxa* C.F. Gaertn. (Sapotaceae) in decreasing order of abundance (Table 1). These species contributed about 57.3% of the total number of individual of plants identified. In contrast the least abundant species were *Bridelia micrantha* Baill., *Daniellia oliveri* (Rolfe) Hutch. & Dalziel, *Ficus* sp., *Gardenia aqualla* Stapf. & Hutch., *Parkia biglobosa* (Jacq.) R.Br.ex G. Don, *Securidaca longepedunculata* Fresen., and *Vitex chrysocarpa* Planch.Eight of the woody plants in the reserve were frequently encountered, i.e., in 50% or more of the plots studied. These species were *Combretum mollis* S. Vidal, *Crossopteryx febrifuga* Benth., *Vitellaria paradoxa* C.F. Gaertn., *Strychnos spinosa* Lam., *Annona senegalensis* Pers., *Grewia venusta* Fresen., *Combretum* sp., and *Pterocarpus erinaceus* Lam. It

Table 1. Species of woody plants, their families, growth-form, abundance, frequency of occurrence and distribution statistics in Singsaglebini Forest Reserve in northern Ghana.

Species	Family	Growth-form	Abundance	Frequency of occurrence	Variance	Distribution statistics (df = 14) Mean	χ^2	Probability	Pattern
Acacia dudgeoni Craib	Fabaceae	Small tree	2	3	0.27	0.13	28	0.014	Aggregated
Acacia gourmaensis A. Chev.	Fabaceae	Tree	24	2	9.10	1.67	76.40	0	Aggregated
Acacia hockii De Wild.	Fabaceae	Small tree	19	1	17.21	1.27	190.21	0	Aggregated
Acacia tortilis Hayne	Fabaceae	Small tree	40	5	35.24	2.67	185	0	Aggregated
Afzelia africana Sm.	Fabaceae	Tree	86	4	342.21	5.73	835.63	0	Aggregated
Annona glauca Schumach. & Thonn.	Annonaceae	Shrub	2	2	0.12	0.13	13	0.53	Random
Annona senegalensis Pers.	Annonaceae	Shrub	55	9	25.10	3.67	95.82	0	Aggregated
Anogessius leiocarpus Guill & Perr.	Combretaceae	Tree	77	7	95.41	5.13	260.21	0	Aggregated
Bombax costatum Pellegr. & Vuillet	Bombacaceae	Tree	4	2	0.64	0.27	33.5	0.0026	Aggregated
Bridelia ferruginea Benth.	Euphorbiaceae	Small tree	19	7	5.78	1.27	63.89	0	Aggregated
Bridelia micrantha Baill.	Euphorbiaceae	Small tree	1	1	0.067	0.067	14	0.45	Random
Burkea africana Hook.	Fabaceae	Small tree	24	4	13.40	1.60	117.25	0	Aggregated
Combretum collinum Fresen	Combretaceae	Small tree	179	4	98.07	11.93	115.05	0	Aggregated
Combretum molle R. Br. ex G. Don.	Combretaceae	Small tree	84	13	26.11	5.60	65.29	0	Aggregated
Combretum nigricans Leprieur ex Guill. & Perr	Combretaceae	Small tree	40	1	39.52	2.67	207.5	0	Aggregated
Combretum sp.	Combretaceae	Small tree	12	9	9.60	0.80	168	0	Aggregated
Crossopteryx febrifuga (Afzel. ex G. Don.) Benth.	Rubiaceae	Tree	56	11	19.50	3.73	73.11	0	Aggregated
Dalbergia afzeliana G. Don	Fabaceae	Tree	150	1	1500.0	10.00	2100	0	Aggregated
Daniellia oliveria (Rolfe) Hutch. & Dalz.	Fabaceae	Tree	1	1	0.067	0.067	14	0.45	Random
Detarium microcarpum Guill. & Perr.	Fabaceae	Tree	32	4	17.12	2.13	112.38	0	Aggregated
Dichrostchys cinerea (L.) Wright & Arn.	Fabaceae	Shrub	339	5	2625.69	22.60	1626.53	0	Aggregated
Entada africana Guill & Perr.	Fabaceae	Small tree	20	6	4.52	1.33	47.5	1.93E-05	Aggregated
Feretia apodanthera Del.	Rubiaceae	Shrub	10	2	5.38	0.67	113	0	Aggregated
Ficus sp	Moraceae	Tree	1	1	0.067	0.067	14	0.45	Random
Gardenia aqualla Stapf. & Hutch.	Rubiaceae	Shrub	1	1	0.067	0.067	14	0.45	Random
Gardenia ternifolia Schum. & Thonn.	Rubiaceae	Shrub	25	7	6.67	1.67	56	8.00E-07	Aggregated
Grewia venusta Fresen.	Tiliaceae	Small tree	41	9	12.35	2.73	63.27	1.00E-07	Aggregated
Hexabolus monopetalus Engl. & Diels.	Annonaceae	Shrub	34	3	26.35	2.27	162.76	0	Aggregated
Hoslundia opposita Vahl	Verbanaceae	Shrub	10	2	5.38	0.67	113	0	Aggregated
Hymenocardia acida Tul.	Euphorbiaceae	Tree	4	2	0.50	0.27	26	0.026	Random
Khaya senegalensis A. Juss.	Meliaceae	Tree	16	1	17.07	1.07	224	0	Aggregated

Species	Family	Growth-form	Abundance	Frequency of occurrence	Variance	Distribution statistics (df =14) Mean	χ^2	Probability	Pattern
Lannea acida A. Rich	Anacardiaceae	Tree	12	3	2.89	0.80	50.5	6.50E-06	Aggregated
Lannea barteri Engl.	Anacardiaceae	Tree	7	5	0.55	0.47	16.57	0.28	Random
Lippia multiflora Moldenke	Verbanaceae	Shrub	2	1	0.27	0.13	28	0.014	Aggregated
Maytenus senegalensis (Lam.) Exell.	Celastraceae	Shrub	3	2	0.31	0.20	22	0.078	Random
Mitragyna inermis (Willd.) Kuntze	Rubiaceae	Tree	19	3	15.07	1.27	166.53	0	Aggregated
Nauclea latifolia Sm.	Rubiaceae	Shrub	15	1	5.14	1.00	72	0	Aggregated
Opilia celtidifolia Endl. ex. Walp.	Opiliaceae	Liana	4	1	1.07	0.27	56	8.00E-07	Aggregated
Papilionaceae	Fabaceae	Tree	35	2	60.24	2.33	361.43	0	Aggregated
Parkia biglobosa (Jacq.) R.Br. ex G.Don	Fabaceae	Tree	1	2	0.067	0.067	14	0.45	Random
Pavetta corymbosa F.N. Williams	Rubiaceae	Shrub	2	1	0.27	0.13	28	0.014	Aggregated
Pericopsis laxiflora (Benth. ex Baker) Meeuwen	Fabaceae	Tree	46	2	70.64	3.067	322.48	0	Aggregated
Piliostigma thonningii (Schumach.) Milne-Redh	Fabaceae	Shrub	13	3	4.41	0.87	71.2308	0	Aggregated
Prosopis africana Taub.	Fabaceae	Tree	3	2	0.31	0.20	22	0.078	Random
Protea madiensis Oliv.	Poteaceae	Shrub	19	2	12.07	1.27	133.37	0	Aggregated
Pseudocedrela kotschyi Harms	Meliaceae	Tree	33	7	15.17	2.20	96.55	0	Aggregated
Pteleopsis suberosa Engl. & Diels	Combretaceae	Small tree	298	5	1953.84	19.87	1376.87	0	Aggregated
Pterocarpus erinaceus Lam.	Fabaceae	Tree	40	8	14.67	2.67	77	0	Aggregated
Rourea coccinea (Schumach. & Thonn.) Hook.f.	Connaraceae	Shrub	116	5	166.92	7.73	302.19	0	Aggregated
Securidaca longependuculata Fresen.	Polygalaceae	Small tree	1	1	0.067	0.067	14	0.45	Random
Securinega virosa (Willd.) Baill.	Euphorbiaceae	Shrub	74	6	98.92	4.93	280.73	0	Aggregated
Stereospermum kunthianum Cham.	Bignoniaceae	Tree	29	5	18.50	1.93	133.93	0	Aggregated
Strychnos innocua Delile.	Loganiaceae	Small tree	7	1	3.27	0.47	98	0	Aggregated
Strychnos spinosa Lam.	Loganiaceae	Small tree	69	9	31.97	4.60	97.30	0	Aggregated
Terminalia avicenoides Guill. & Perr.	Combretaceae	Small tree	20	3	15.38	1.33	161.5	0	Aggregated
Terminalia macroptera Guill. & Perr.	Combretaceae	Tree	29	2	26.92	1.93	194.97	0	Aggregated
Terminalia mollis S.Vidal	Combretaceae	Tree	115	7	207.10	7.67	378.17	0	Aggregated
Trichilia emetica Vahl	Meliaceae	Tree	13	1	11.27	0.87	182	0	Aggregated
Vitellaria paradoxa C.F. Gaertn.	Sapotaceae	Tree	84	9	131.69	5.60	329.21	0	Aggregated
Vitex chrysocarpa Planch.	Verbanaceae	Shrub	1	1	0.067	0.067	14	0.45	Random
Vitex doniana Sweet	Verbanaceae	Shrub	6	1	2.40	0.40	84	0	Aggregated
Xerroderis stuhlamanii (Taub.) Mendonca & E.P. Sousa	Fabaceae	Tree	10	3	2.52	0.67	53	2.60E-06	Aggregated

Table 2. Families of woody plants, their species richness and abundance in the Singsaglebini Forest Reserve in northern Ghana.

Family	Species richness (number of species)	Relative species richness	Abundance (number of individuals)	Relative abundance
Anacardiaceae	3	4.8	32	1.3
Annonaceae	3	4.8	91	3.6
Bignoniaceae	1	1.6	29	1.1
Bombacaceae	1	1.6	4	0.16
Celastraceae	1	1.6	3	0.12
Combretaceae	9	14.5	854	33.7
Connaraceae	1	1.6	116	4.6
Euphorbiaceae	4	6.5	98	3.9
Fabaceae	18	29.0	886	35.0
Loganiaceae	2	3.2	76	3.0
Meliaceae	2	3.2	49	1.9
Moraceae	1	1.6	1	0.04
Opiliaceae	1	1.6	4	0.16
Polygalaceae	1	1.6	1	0.04
Poteaceae	1	1.6	19	0.75
Rubiaceae	7	11.3	127	5.0
Sapotaceae	1	1.6	84	3.3
Tiliaceae	1	1.6	41	1.6
Verbanaceae	4	6.5	19	0.75

thus follows that the most abundant woody plants in the reserve were not necessarily the most frequently encountered plants.

The result of the analysis of the general pattern of distribution of the woody plant community in the reserve shows that the species were highly aggregated (χ^2 =12465.8, df = 930, P = 0). The distribution of the individual woody plant species was highly discordant with respect to each other (χ^2 = 11746.5, df = 916, P= 0) whiles individual species were found to be highly aggregated in the plots (χ^2 = 719.3, df =14, P = 0). The majority (80.6%) of the individual woody plant species were found to be aggregated in their pattern of distribution in the reserve (Table 1). In contrast, twelve of the species, namely, *Annona glauca* Schumach. & Thonn., *Bridellia micrantha* (Hochst.) Baill. *Daniellia oliveria*, *Ficus* sp., *Gardenia aqualla*, *Maytenus senegalensis* (Lam.) Exell., *Hymenocardia acida* Tul., *Lannea barteri* Engl., *Parkia biglobosa*, *Prosopis africana* Taub., *Securidaca longependuculata*, and *Vitex chrysocarpa* showed some degree of randomness in the pattern of distribution in the reserve.

DISCUSSION

Most of the species of plants identified in the Sinsabligbini Forest Reserve in northern Ghana are species that have been reported in other guinea savanna areas elsewhere in Ghana (Lawson et al. 1969; Brookman-Amissah et al. 1980; Oteng-Yeboah 1996; Asase & Oteng-Yeboah 2007). However, a few of the species such as *Rourea coccinea* (Schumach &. Thonn.) Hook.f., *Dalbergia africana*, and *Hoslundia opposita* Vahl that were identified in the reserve have not been reported in other areas in the Guinea Savanna Zone of Ghana based on survey of the available literature. Similarly, some of the common woody plant species such as *Balanities aegyptiaca* Sands. and *Ximenia americana* L. that have been reported in other areas of the Guinea Savanna Zone of Ghana were not identified in the reserve. This finding has confirmed that the floristic composition of the savanna is immensely variable even over relatively homogeneous areas (Hopkins 1979; Lawson 1985).

The high species richness and abundance of taxonomic families such as Fabaceae, Combretaceae, Rubiaceae, and Anacardiaceae in the guinea savanna has been noted elsewhere (Hopkins 1979; Asase & Oteng-Yeboah 2007). In a study of three traditional groves in northern Ghana, Oteng-Yeboah (1996) also

reported on the predominance of members of the Fabaceae (Caesalpinaceae, Papilionaceae, and Mimosaceae), Combretaceae, Rubiaceae in the different groves which report is similar to the results of this study. It is also interesting to note that even though some of the families such as Verbenaceae and Anacardiaceae were found to have several species, their individual plant representation were very low. On the other hand, there were more individual members of some of the families with lower species numbers such as Connaraceae and Sapotaceae. It thus follows that not all the families with many species are abundant in the reserve. It is important to note that some of the important guinea savanna trees such as *Afzelia africana* Sm., *Daniellia oliveria*, and *Parkia biglobosa* (Hopkins 1979; Lawson 1985) were not abundant in the reserve.

In a study of the pattern of distribution of some woody plants in the Olokemeji Forest Reserve in Nigeria, Greig-Smith (1991) noted that patchiness could be explained as a response to factors such as soil differences, pattern of previous farming, intensity of burning from wild fires and at the smallest scale interference between individual plants possibly due to competition for water. We found evidence of annual wild bush fires and farming activities in the reserve and these factors might also explain the pattern of distribution of the woody plants in the reserve. As yet there are no reports on the patterns of distribution of savanna plants in Ghana and so no comparisons could be made.

To conclude, the present study is the first publication on the species of plants found in the Sinsabligbini Forest Reserve in northern Ghana. The study has shown that the characteristics of the vegetation in the reserve were generally similar to that of other guinea savanna areas. It has also shown that the floristic composition and abundance of species in different areas of the Guinea Savanna Zone is very variable. Thus there is a case for the study of the diversity of plants found in the different areas of the Guinea Savanna Zone of Ghana in order to support the conservation of savanna botanical resources especially for specific areas of the Guinea Savanna Zone in Ghana.

ACKNOWLEDGMENTS

We are most grateful to the communities living around the reserve for their hospitality during fieldwork. We are also thankful to Messer's Francis Chimsah and John Baba of the University for Development Studies (UDS) in Ghana for their assistance in the field. This study was supported by the Northern Savanna Biodiversity Conservation Project (NSBCP) in Ghana funded by the World Bank. We also thank Alfred Oteng-Yeboah for a critical review of this paper.

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NEW STATE RECORDS OF VASCULAR PLANTS FOR THE SOUTHERN ROCKY MOUNTAIN REGION

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ABSTRACT

Four state records of three vascular plant species are reported for the Southern Rocky Mountain region. *Amaranthus californicus* is newly recorded for Colorado and New Mexico, whereas *Euphorbia extipulata* and *Trifiolium dasyphyllum* var. *anemophilum* are documented for the first time in Colorado.

RESUMEN

Se citan tres plantas vasculares para algún estado de la parte sur de la regiÓn de las Montañas Rocosas. *Amaranthus californicus* es citada nuevamente para Colorado y Nuevo México, mientras que *Euphorbia extipulata* y *Trifiolium dasyphyllum* var. *anemophilum* se documentan por primera vez en Colorado.

INTRODUCTION

Routine identifications during the past few years of specimens housed in the herbarium at the University Northern Colorado Herbarium (GREE), where the authors previously worked, revealed new state records of vascular plants for Colorado and New Mexico, which we report here. All specimens are housed at GREE (herbarium acronyms following Holmgren & Holmgren 1998) except for the specimen of *Trifolium* (at COLO), and were compared against holdings at GREE, CS, COLO, or RM. Nomenclature and family designations follow Snow (2009).

AMARANTHACEAE

Amaranthus californicus (Moq.) S. Wats. This species is a glabrous, prostrate, monoecious annual that occupies seasonally moist flats, shores and other disturbed habitats at elevations between 0–2800 m (Mosyakin & Robertson 2003; Welsh et al. 2003). We report it here for the first time from Colorado and New Mexico; various sources also report the species from Canada, California, Idaho, Kansas, Montana, Nebraska, Nevada, Oregon, South Dakota, Texas, Utah, Washington and Wyoming.

Voucher specimen: **COLORADO. Weld Co.:** T09N R65W S20 SE, <0.2 mi N of Weld County Road 102, ca. 6 air mi E of Hwy 85, elev. ca. 5160 ft [1573 m], infrequent in alkali bed of Little Owl Creek, Pawnee National Grassland, 10 Sep 2004, *D.L. Hazlett 12159.* **NEW MEXICO. San Miguel Co.:** elev. ca. 6000 ft in a dry lake be, 15 Aug 1944, *A.L. Hershey s.n.*

EUPHORBIACEAE

Euphorbia exstipulata Engelm. In the Southern Rockies this annual species was collected only once previously, in 1894, in Platte Co. Wyoming (Dorn 2001). It is noted as likely extirpated for the State of Wyoming (Kartesz 2009). An additional collection near our area is known from Cimarron County, Oklahoma, but the species otherwise occurs in the USA in UT, AZ, NM, TX, and CA (Kartesz 2009).

Voucher specimen: **COLORADO. Baca Co.:** Ravine 10 mi SW of Campo, May–Sep 1977–1978, *W.E. Harmon 9507.*

FABACEAE

Trifolium dasyphyllum Torr. & A. Gray var. **anemophilum** (Greene) J.S. Martin ex Isley. This native perennial previously has been known only from Wyoming. The closest population occurs in the Laramie Range in eastern Albany County, Wyoming (Isley 1980).

Voucher specimen: **COLORADO. Weld Co.:** T10N R60W S4, 7 mi E of Grover, elev. ca. 1646 m, infrequent (in rock crevice) on N-facing rocky ridge (private land), 04 Jun 1999, *D.L. Hazlett 10924* (COLO).

ACKNOWLEDGMENTS

Support for curatorial work of Southern Rocky Mountain taxa at GREE was supported by NSF DEB-0237149. Thanks to an anonymous reviewer, Ronald Hartman, and Ben Legler for reviewing the manuscript, and to John Kartesz for providing advance copies of Version 2 of the *Floristic Synthesis*.

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PYRACANTHA KOIDZUMII (ROSACEAE) NEW TO THE ARKANSAS FLORA

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ABSTRACT

Pyracantha koidzumii (Hayata) Rehder (Formosa firethorn) is here reported as new to the Arkansas flora. Additionally, it is also probably the first record of the genus *Pyracantha* growing spontaneously in the state. A key and illustrations of the three most commonly encountered species of *Pyracantha* outside of cultivation in the US are included.

RESUMEN

Pyracantha koidzumii (Hayata) Rehder (Formosa firethorn) is here reported as new to the Arkansas flora. Additionally, it is also probably the first record of the genus *Pyracantha* growing spontaneously in the state. A key and illustrations of the three most commonly encountered species of *Pyracantha* outside of cultivation in the US are included.

INTRODUCTION

At present, non-native species comprise approximately 21% of the Arkansas flora (Arkansas Vascular Flora Committee 2006), with new species of non-native plants continuously being documented and added (Peck 2003; Peck & Serviss 2006; Serviss et al. 2006, 2008a, 2008b; Serviss & Peck 2008). Many of the species comprising these most recent records were well established when initially encountered; therefore, it is extremely important to record first encounters with escaped populations and monitor these new spontaneous occurrences of non-native species to evaluate their potential for becoming the next wave of invasive species (Yatskievych & Raveill 2001).

Pyracantha is a Eurasian genus consisting of about 10 species of woody, evergreen, thorny shrubs and trees (Bailey 1971; Flora of China Editorial Committee 2003; Krüssmann 1978). Species of *Pyracantha* are important as ornamentals because of their evergreen habit, and bright red, orange, or yellow-colored fruits that persist well into winter. Several species of *Pyracantha* have become established to various degrees across much of the southern US from California to Florida and the Carolinas (NRCS 1999), but until now, have not been recorded outside of cultivation in Arkansas.

Pyracantha coccinea (D. Don) M.J. Roem. (scarlet firethorn) was previously documented for Arkansas (Arkansas Vascular Flora Committee 2006). However, this record now appears to be of questionable status regarding its position in the flora, as further investigation has led to the possibility that the specimen cited in the checklist may have simply been persisting from cultivation; and not actually spontaneous. As a result, it will apparently not be included in the upcoming atlas for the vascular flora of Arkansas (Brent Baker, pers. comm.). Additionally, a second possible record of *Pyracantha* in the state collected from Lafayette County in 1959 by Demaree (*41944*; UMO), was examined by the author and determined to be *Crataegus* (hawthorn). Subsequently, the record of *P. koidzumii* presented here is currently the only definitive record of this genus occurring outside of cultivation in Arkansas.

SPECIMEN RECORD OF *P. KOIDZUMII* FOR ARKANSAS

Pyracantha koidzumii (Hayata) Rehder (*P. formosana* Kanehira) (Rosaceae). Formosa firethorn is a large, evergreen shrub or small tree to about 4(5.5) m in height that is native to Taiwan. In addition to Arkansas, Formosa firethorn has been documented outside of cultivation in the US in Alabama, Arizona, Florida, Georgia, and South Carolina, as determined from the national flora database kept by NRCS (1999).

J. Bot. Res. Inst. Texas 3(1): 319 – 321. 2009

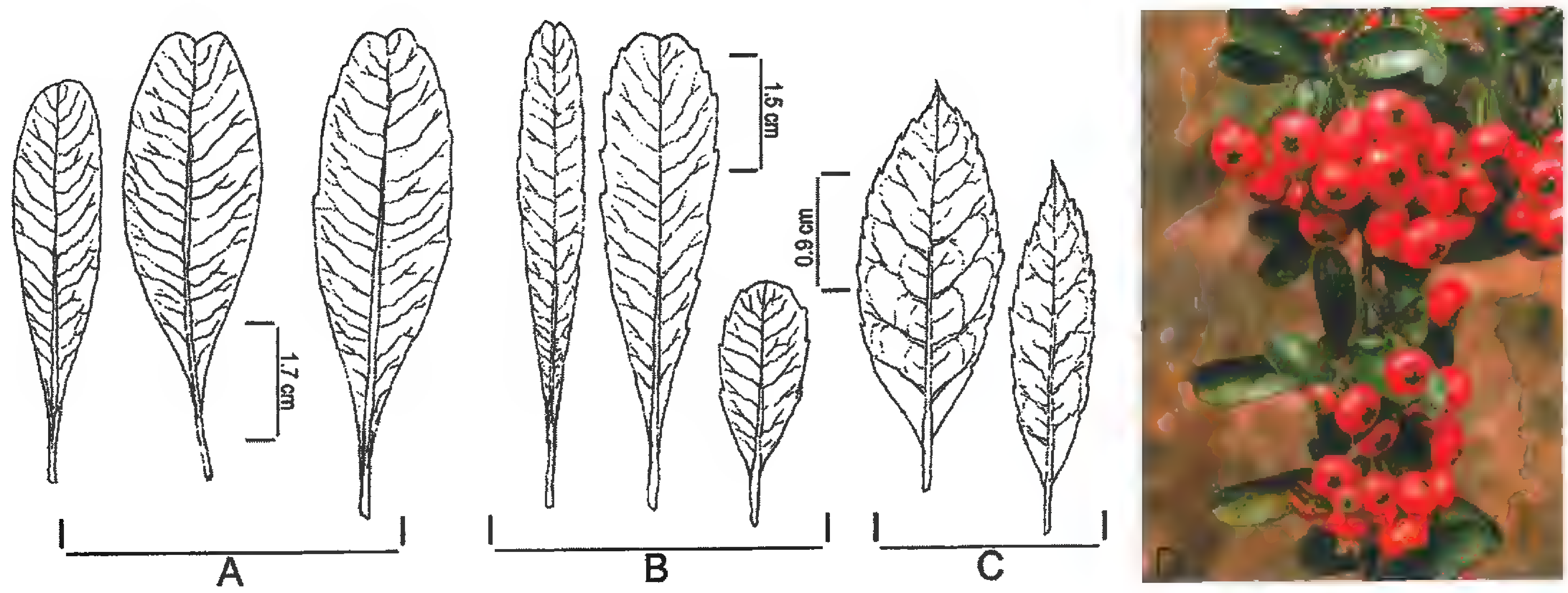

Fig. 1. Photograph of *P. koidzumii* and leaf illustrations (for comparison) of three *Pyracantha* species, including *P. koidzumii*. A. *Pyracantha koidzumii*. B. *Pyracantha fortuneana*. C. *Pyracantha coccinea*. D. *Pyracantha koidzumii* mature fruits and leaves.

Voucher specimen: **Garland Co.:** one arborescent, reproductive-age plant (mature fruits present), steep bluff with rocky soil, semi-disturbed, upland woods habitat, woody associates include: *Liquidambar styraciflua*, *Quercus velutina*, *Nyssa sylvatica*, *Pinus echinata*, *Pinus taeda*, *Prunus serotina*, *Ulmus alata*, and one plant of *Pyrus calleryana*, ca. one-half block N of Central Avenue, 4500 block, Hot Springs, 1 Nov 2008, *B. Serviss and A. Serviss 7396* (HEND).

Many species of *Pyracantha* are difficult to distinguish without careful scrutiny; thus the following key has been provided as an aid to identification. In addition to the approximately 10 currently recognized species in the genus, numerous interspecific hybrids and cultivars also occur. No attempt to treat these additional taxa is made here (for a list and descriptions of many of the hybrids and cultivars of *Pyracantha*, see Krüssmann 1978).

KEY TO *PYRACANTHA* SPECIES LIKELY ENCOUNTERED IN ARKANSAS

At least three species of *Pyracantha*: *P. coccinea*, *P. fortuneana* (*P. crenatoserrata*), and *P. koidzumii*, (Fig. 1) are cultivated in the state, and spontaneous seedlings are sometimes observed in the vicinity of cultivated plants (Serviss 2006).

1. Leaves usually elliptic, sometimes narrowly so, apex acute, margins toothed ____ **P. coccinea**
1. Leaves usually oblong, oblanceolate, or obovate-oblong, apex obtuse, rounded, or nearly truncate, sometimes emarginate, margins toothed or entire (leaves of *P. koidzumii* can be elliptic, but with entire margins).
    2. Leaf margins on most or all leaves conspicuously toothed, leaves generally widest toward apex ____ **P. fortuneana**
    2. Leaf margins entire, a few leaves may have a few widely spaced teeth, leaves generally widest more toward the middle ____ **P. koidzumii**

Pyracantha can sometimes be confused with certain species of *Crataegus*, but differs from it by its evergreen habit, leafy thorns, and two fertile ovules per carpel. *Crataegus* species are deciduous with leafless thorns and only one fertile ovule per carpel. The generally narrow, unlobed, finely-toothed leaves of *Pyracantha* can also be useful in distinguishing it from *Crataegus*.

ACKNOWLEDGMENTS

I would like to sincerely thank my daughter, Annabelle Serviss, who initially discovered and brought to my attention the *P. koidzumii* plant, Brent Baker (University of Arkansas) for providing information regarding the current status of *Pyracantha* in Arkansas, Robin Kennedy (University of Missouri at Columbia) for providing a specimen loan, Guy Nesom (University of Texas at Austin), Victor Maddox (Mississippi State University), and one anonymous reviewer for their helpful comments and suggestions regarding this paper, and the Henderson State University Biology Department for supporting this research.

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BOOK NOTICE

Hideaki Ohba, Yu Iokawa, and Lokendra Raj Sharma (eds.). 2008. **Flora of Mustang, Nepal.** (ISBN 978-4-906464-15-9, hbk.). Kodansha Scientific Ltd., 9-25 Shin-ogawa-cho, Shinjuku-ku, Tokyo, Japan. (**Orders:** www.amazon.co.uk). $106.00, 483 pp., index, color plates, b&w figures and line drawings, 7" x 10 1/4".

From the preface: "The Nepal Himalaya is of immense interest to botanists due to its rich biodiversity. All global bioclimatic zones are juxtaposed along the slopes of the Nepalese mountains...The Mustang region is of special interest for its aridity and high degree of floral endemism ... It is a nearly treeless region and its flora and vegetation are Tibetan in character."

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2. Vegetation of Mustang
3. Climatic Conditions of Mustang
4. Floristic Synopsis and Plant Geography
5. A Systematic List of the Collections

   PTERIDOPHYTA

   Equisetaceae, Parkeriaceae, Aspleniaceae, Dryopteridaceae, Woodsiaceae

   SPERMATOPHYTA-GYMNOSPERMAE

   Ephedraceae, Pinaceae, Cupressaceae

   SPERMATOPHYTA-DICOTYLEDONEAE-ARCHICHLAMYDEAE

   Salicaceae, Betulaceae, Urticaceae, Santalaceae, Polygonaceae, Nyctaginaceae, Carypohyllaceae, Chenopodiaceae, Ranunculaceae, Circaeasteraceae, Berberidaceae, Papaveraceae, Cruciferae, Crassulaceae, Saxifragaceae, Hydrangeaceae, Rosaceae, Leguminosae, Geraniaceae, Zygophyllaceae, Linaceae, Euphorbiaceae, Polygalaceae, Balsaminaceae, Thamnaceae, Malvaceae, Thymelaeaceae, Elaeagnaceae, Violaceae, Tamaricaceae, Onagraceae, Umbelliferae

   SPERMATOPHYTA-DICOTYLEDONEAE-SYMPETALAE

   Ericaceae, Primulaceae, Oleaceae, Gentianaceae, Asclepiadaceae, Rubiaceae, Convolvulaceae, Boraginaceae, Labiatae, Solanaceae, Scrophulariaceae, Bignoniaceae, Orobanchaceae, Lentibulariaceae, Plantaginaceae, Caprifoliaceae, Dipsacaceae, Campanulaceae, Compositae

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MEDICAGO RIGIDULA AND *M. TRUNCATULA* (FABACEAE): NEW TO THE CALIFORNIA FLORA

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ABSTRACT

Medicago rigidula and *M. truncatula* are reported for the first time for California. These species have likely become established from rangeland, forage and cover crops grown over the past century. They can be confused with the relatively common *M. polymorpha*, and are probably more widespread than current records indicate.

Key Words: biological invasions, grasslands, *Medicago rigidula*, *Medicago truncatula*, medics, nonnative plants

RESUMEN

Medicago rigidula y *M. truncatula* se reportan por primera vez en California. Probablemente estas especies se han establecido a través de los pastizales de forraje y los cultivos de cobertura sembrados durante el siglo pasado. *Medicago rigidula* y *M. truncatula* pueden ser confundidas con la especie relativamente común *M. polymorpha*, y probablemente están más generalizadas que lo indicado por los registros actuales.

Annual species of *Medicago*, commonly known as medics, are indigenous to the Mediterranean region, and some of these have become established in temperate and Mediterranean-type climate regions around the world (Heyn 1963; Piano & Francis 1992). In this paper, we provide the first documented records of *Medicago rigidula* (L.) All. and *M. truncatula* Gaertn. for California.

Medicago rigidula (Tifton medic, Tifton burclover, Tifton bur medic, rigid medic) and *M. truncatula* (barrel medic, barrel clover) have not been reported previously in major publications addressing nonnative species in California (Isely 1993; Bossard et al. 2000; Hrusa et al. 2002; Bossard & Randall 2007; DiTomaso & Healy 2007; Jepson Flora Project 2008; USDA 2008a, b). They have also not been included in treatments of the Fabaceae in county floras or in recent local floristic studies covering coastal southern California (Boyd 2001; Schneider-Ljubenkov & Ross 2001; Bowler & Bramlet 2002; Wishner 2002; Bowler & Elvin 2003; Pyke et al. 2003; Roberts et al. 2004; Rebman & Simpson 2006; Clarke et al. 2007; Roberts & Bramlet 2007; Roberts et al. 2007; Roberts 2008).

Voucher specimens:

Medicago rigidula (Fabaceae, Trifolieae, Trigonellinae), **U.S.A. CALIFORNIA. Orange Co.:** City of San Juan Capistrano, San Juan Creek Rd. at San Juan Creek Circle, UTM (NAD 83) 11S 0439671E 3706917N, elev. ca. 24 m, uncommon in annual grassland, 18 Mar 2007, *Riefner 07-150* (RSA); City of Laguna Niguel, Laguna Niguel Regional Park, general vicinity of La Paz Rd. at Aliso Creek, UTM (NAD 83) 11S 0434480E 3712053N, elev. ca. 70 m, uncommon, disturbed roadside, 1 Apr 2007, *Riefner 07-165* (DAO, RSA); City of San Juan Capistrano, San Juan Creek area, ca. 0.2 mi W of intersection of Paseo Tirador and Calle Arroyo St., UTM (NAD 83) 11S 0439010E 3706660N, elev. ca. 31 m, uncommon in open field, 1 May 2008, *Riefner 08-73* (DAO, RSA); Ladera Ranch, Cecil Pasture at Jerome Rd., UTM (NAD 83) 11S 0439962E 3713383N, elev. ca. 157 m, uncommon along Bluff Top Trail in annual grassland, 12 May 2008, *Riefner 08-75* (DAO); City of San Juan Capistrano, 0.2 mi E of Antonio Pkwy. on Hwy. 74 (Ortega Hwy.), UTM (NAD 83) 11S 0442824E 3709137N, elev. ca. 88 m, uncommon in annual grassland and disturbed sage scrub, 19 May 2008, *Riefner 08-99* (RSA); unincorporated land located between the Cities of Lake Forest and Rancho Santa Margarita, El Toro Rd. near Meadow Ridge Dr., UTM (NAD 83) 11S 0442282E 3725738N, elev. ca. 362 m, rare along fire break with ruderal vegetation, 22 May 2008, *Riefner 08-120* (RSA).

Medicago truncatula (Fabaceae, Trifolieae, Trigonellinae), **U.S.A. CALIFORNIA Orange Co.:** City of Laguna Niguel, Laguna Niguel Regional Park, general vicinity of La Paz Rd. at Aliso Creek, UTM (NAD 83) 11S 0434480E 3712053N, elev. ca. 70 m, uncommon in *Atriplex* scrub, 1 Apr 2007, *Riefner 07-166* (DAO, RSA); City of Laguna Niguel, Laguna Niguel Regional Park, general vicinity of La Paz Rd. at Aliso Creek, UTM (NAD 83) 11S 0434316E 3712082N, elev. ca. 63 m, uncommon in *Distichlis* grassland (plant with conspicuous,

reddish, diamond-shaped mark in center of each leaflet lamina), 1 Apr 2007, *Riefner 07-168* (DAO); City of Orange, SW portion of Irvine Regional Park, Irvine Park Rd., UTM (NAD 83) 11S 0431403E 373509N, elev. ca. 188 m, uncommon in disturbed and ruderal habitats, 12 Apr 2007, *Riefner 07-178* (DAO, RSA); City of Rancho Santa Margarita, Tijeras Canyon, N ca. 0.5 mi from Meandering Trails Rd. on Antonio Pwky., UTM (NAD 83) 11S 0442289E 3718077N, elev. ca. 221 m, uncommon in annual grassland, 24 March 2008, *Riefner 08-64* (RSA); City of San Juan Capistrano, 0.2 mi E of Antonio Pkwy. on Hwy. 74 (Ortega Hwy.), UTM (NAD 83) 11S 0442824E 3709137N, elev. ca. 88 m, uncommon, roadside and annual grassland, 19 May 2008, *Riefner 08-92* (DAO, RSA).

Medicago rigidula sensu lato is native to Eurasia and North Africa (Small & Jomphe 1989; Small et al. 1990). The European and African populations have been segregated as *M. rigiduloides* E. Small, based particularly on pollen morphology and fruit characters (Small 1990; Small et al. 1990). Additional studies confirming separation of these taxa are needed (Heft & Groose 1996), so we have not attempted to identify the California collections with respect to these groups. *Medicago truncatula* is also indigenous to Eurasia and North Africa (Small & Jomphe 1989; Small et al. 1990; Small et al. 1991). With the exception of *M. polymorpha* L., it is the most common weedy annual *Medicago* in the Old World (Small & Jomphe 1989).

Medicago rigidula and *M. truncatula* grow on a variety of soils, ranging in texture from sandy loams to clay, and the former is adapted to rocky soils; both species are best adapted to neutral to somewhat alkaline (pH 6 to 9) conditions (Small & Jomphe 1989; Nair et al. 2006; Frame 2008). The annual medics are not cold hardy and will die after a killing frost (Quinlivan et al. 1986). However, *M. rigidula* is relatively cold tolerant (Walsh et al. 2001; Small & Jomphe 1989; Krall et al. 1996). Although not widely recognized as a halophyte, *M. truncatula* performed very well in an experimental study of cover crops suitable for saline soils of California's Great Central Valley (Mitchell 1996).

Medicago species are among the legumes that are highly selective of rhizobial bacteria, which have important nitrogen fixing properties (Allen & Allen 1981). The annual species of *Medicago* are highly adapted to a wide range of environments and to new locations (Crawford et al. 1989). Accordingly, many annual medics now play an important agronomic role in dryland farming around the world (Walsh et al. 2001). The annual medics comprise the principal legume component of pasture lands on more than 20 million ha in Southern Australia where they are utilized as self-seeding annuals to improve soil structure, increase soil nitrogen, and provide forage for livestock (Cocks et al. 1980; Crawford et al. 1989; Squires & Tow 1991). *Medicago truncatula* is a highly valued and widely cultivated species in Australia and other Mediterranean climate regions around the world (Crawford et al. 1989; Walsh et al. 2001; Nair et al. 2006). There are more cultivars of *M. truncatula* than of any other *Medicago* except *M. sativa* L. (alfalfa). *Medicago truncatula* is also being developed as a model legume plant in both classical and molecular genetic studies to elucidate the functions of its genes (e.g., bacterial and fungal symbiosis, stress resistance, and plant architecture) and to exploit its genome (e.g., improved seed quality and production of specific secondary metabolites); for recent reviews see Thoquet et al. (2002) and Watson et al. (2003). By contrast, *M. rigidula* has attracted relatively limited interest as an agricultural crop, and there are few cultivars.

In coastal southern California, ranchers have long prized burr clover (*M. polymorpha*) as valuable forage (U.S. Coast & Geodetic Survey 1891). Several other annual medics, including *M. arabica* (L.) Huds., *M. lupulina* L., *M. rigidula*, *M. scutellata* Mill., *M. truncatula*, and *M. turbinata* (L.) All. were tested in row nurseries or broadcast plots in order to improve forage on California rangelands, including four sites in Orange County, southern California (Jones & Love 1945). These species did not perform well during the early field tests, and were not recommended for use on rangelands in the South Coast region (Jones & Love 1945). However, following the successful breeding and development of numerous cultivars and experimental genotypes, many annual species of *Medicago*, including *M. rigidula* and *M. truncatula*, have been successfully re-evaluated for use and/or are currently utilized as cover crops or forage in the United States (Allen & Allen 1981; Zhu et al. 1996; Shrestha et al. 1998; Fisk et al. 2001; Walsh et al. 2001; Krall et al. 2007). In California, the annual medics are favored as cover crops in no-till orchards and vineyards, especially in the Great Central Valley (Miller et al. 1989; UC SAREP 2008). Despite their widespread use, *M. rigidula* and *M. truncatula* have been rarely reported growing outside of cultivation in the United States (Kartesz & Meacham 2005; Jepson Flora Project 2008; USDA 2008a, b).

There are several reasons why the annual medics should be expected as introduced weeds in California. All of the dozen or so cultivated medics are weeds in the Old World, and have the potential to be weedy elsewhere. The cultivars that are often grown experimentally or for their proven value in California are scarcely different from their wild progenitors. In addition, essentially wild plants are also often cultivated. Accordingly, the annual medics have not been weakened by domestication.

Also, the majority of the annual species of *Medicago* have spiny pods adapted to adherence to fur and feathers, which are easily distributed by wild animals, and also by humans (for example, in wool). Their seeds are well protected in indehiscent, spiny pods, and are long lived. A seed of *M. polymorpha* extracted from adobe brick from Mexico, estimated to be of the order of 200 years of age, successfully germinated (Spira & Wagner 1983). Therefore, it would not be surprising to find annual medics naturalized in California.

Southern Orange County supports ideal conditions that have facilitated the introduction and naturalization of annual medics, which include: a Mediterranean-type climate; widespread neutral to alkaline sandy loam to clay soils; extensive historic ranchos supporting cattle grazing, dryland row crops, orchards, and equestrian uses; and expanding residential/commercial land development that has split up the historic ranchos, increased disturbance, and facilitated invasions of new weed species in the region (Wachtell 1978; Hallan-Gibson et al. 2005; Orange County Historical Society 2005; Riefner & Boyd 2007). Notably, access to historic grazing habitats in southern Orange County is now possible owing to lands dedicated to open space and conservation, most of which have been poorly studied (Roberts & Bramlet 2007).

Some medic cultivars are characterized by single, reddish, adaxial leaflet marks (Nair et al. 2006), although this phenomenon is relatively rare among most wild medic species. Some of the plants collected in Orange County (*Riefner 07-168*, DAO) have such marks, which may reflect origin from agricultural cultivars. Many of the medic cultivars have been selected for resistance to aphids and root-lesion nematodes, and adaptations to specific soil textures (Nair et al. 2006). Early introductions of *M. rigidula* and *M. truncatula* failed to establish, perhaps because of lack of suitable adaptations, but continued releases of cultivated strains may have led to hybridization and the production of invigorated populations, aiding naturalization in southern California. The introduction of cultivars has been hypothesized to contribute new genetic diversity that could enhance or aid the establishment of nonnative plants (Cox 2004).

In Eurasia, it is extremely common for several species of annual *Medicago* to grow together as weeds. In Orange County, *M. rigidula* and *M. truncatula* are closely associated with *M. polymorpha*, which is the most commonly collected medic in southern California and the most likely to be confused with either *M. rigidula* or *M. truncatula*. *Medicago rigidula* and *M. truncatula* are members of section *Spirocarpos* Ser. subsection *Pachyspirae* (Urb.) Heyn, which is characterized by pods that at maturity are extremely hard, and have alveolar (appearing spongy) tissue on the coil faces (and at the base of spines) that often obscures the coil venation (Small & Jomphe 1989). *Medicago rigidula* pods are usually covered with velvety-glandular hairs (observable in young pods), are discoid, cylindrical, ovoid or spherical in shape, often have evident inter-coil gaps on mature pods, and have radial veins that are strongly curved with limited anastomosing (Heyn 1963; Small & Jomphe 1989; Bena et al. 1998). *Medicago truncatula* has cylindrical pods, usually with a few simple trichomes (often on the spines), long curved spines that frequently point towards the ends of the pod, and weakly to moderately curving radial veins on the coil faces, with limited anastomosing (Heyn 1963; Small & Jomphe 1989; Bena et al. 1998). Occasionally, plants of *M. truncatula* and *M. rigidula* have pods without spines, and both species have moderately pubescent herbage.

Medicago polymorpha, of section *Spirocarpos* (= subsection *Leptospirae* (Urb.) Heyn), is generally glabrous to lightly hispid, and the pods, spiny or rarely merely with tubercles, generally have conspicuous reticulate venation on the coil faces. However, *M. polymorpha* frequently mimics species of *Pachyspirae* in developing very hard pods with proliferating tissue on the fruit coil faces, making identification difficult (Small & Jomphe 1989). This mimicry does not occur in young pods, which should be examined for positive identification. Typical pods of *M. rigidula*, *M. truncatula*, and *M. polymorpha*, and venation on coil faces are depicted in Figure 1.

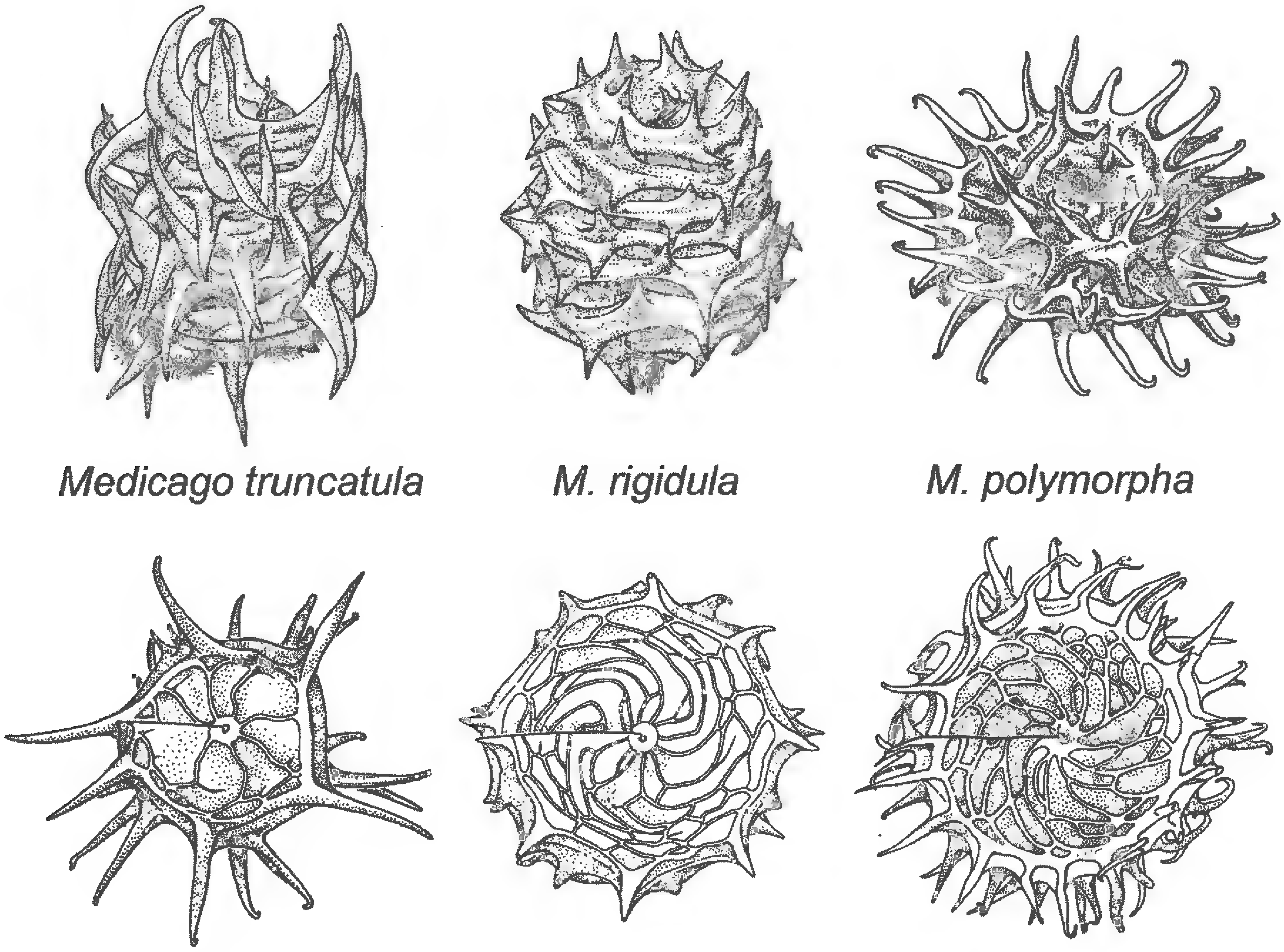

Fig. 1. Typical fruits (top row) and coil faces (bottom row) of *Medicago* species discussed in text. *Medicago truncatula* characteristically has a few simple hairs on the fruits (often on the spines) while *M. rigidula* pods are typically covered with a velvety surface of gland-tipped hairs; venation of the coil faces of these species is obscured by a sponge-like tissue at maturity. Occasionally the venation of pods of *M. polymorpha* is similarly obscured. Length and orientation of spines are variable in these taxa. (All fruits shown are about 1 cm wide. Illustrator: Lucy Yuzyk)

Given the difficulty of discriminating *M. rigidula* and *M. truncatula* from the widespread *M. polymorpha*, it may be that the species reported here as new to California could be established in other agricultural regions of the State, including the Great Central Valley and the Imperial Valley, where there are extensive, suitable habitats.

Note.—After the manuscript was accepted for publication, we identified the two voucher specimens of "*Medicago muricata* All." cited in Dean et al. (2008) (collections made by G. Butterworth in 2005 from San Luis Obispo Co.) as *M. truncatula* Gaertn.

ACKNOWLEDGMENTS

We greatly appreciate the efforts of Harvey Brenneise and Irene Holiman (Library of Rancho Santa Ana Botanic Garden) for assistance with document retrieval. George W. Cox (San Diego State University) and an anonymous reviewer provided helpful comments that greatly improved the manuscript. We also thank Fred Hrusa (California Department of Food and Agriculture, CDA) for a loan of specimens.

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BOOK NOTICE

Douglas J. Futuyma, H. Bradley Shaffer, and Daniel Simberloff (eds.). 2008. **Annual Review of Ecology, Evolution, and Systematics, Volume 39.** (ISSN 1543-592X; ISBN 978-0-8243-1439-2, hbk). Annual Reviews, Inc., 4139 El Camino Way, P.O. Box 10139, Palo Alto, California 94303-0139, U.S.A. (**Orders:** www.AnnualReviews.org, science@annualreviews.org, 800-523-8635, 650-493-4400). $84.00 indiv., 674 pp., 7 5/8" × 9 3/8".

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Cumulative Index of Chapter Titles, Volumes 35–39

NEW AND NOTEWORTHY PLANTS FROM FLORIDA

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ABSTRACT

Four taxa are reported as new to continental United States and the state of Florida: *Azolla pinnata* subsp. *asiatica*, *Melochia nodiflora*, *Ochna serrulata*, and *Passiflora vitifolia*. The reports for the non-native *Lamium purpureum*, *Sida urens*, and *Sphaeropteris cooperi*, and the native *Crataegus opaca*, *Cyperus bipartitus*, *Cyperus eragrostis*, and *Geranium maculatum* are the first for Florida. Here the occurrence of *Torilis arvensis* in Florida is verified (for a total of 12 new records for Florida), and 37 taxa representing significant collections are reported.

RESUMEN

Se citan cuatro taxa como nuevos para los Estados Unidos en la parte continental y el estado de Florida: *Azolla pinnata* subsp. *asiatica*, *Melochia nodiflora*, *Ochna serrulata*, y *Passiflora vitifolia*. Las citas de las alóctonas *Lamium purpureum*, *Sida urens*, y Sphaeropteris *cooperi*, y las nativas *Crataegus opaca*, *Cyperus bipartitus*, *Cyperus eragrostis*, y *Geranium maculatum* son las primeras para Florida. Se verifica aquí la presencia de *Torilis arvensis* in Florida (con un total de 12 nuevas citas para Florida), y se citan 37 taxa que representan colectas importantes.

INTRODUCTION

Recent field work throughout the state of Florida has resulted in the discovery of 12 taxa previously unreported for the state. An additional 37 taxa are reported here as significant collections that either confirm a previously reported taxon's presence here (second and third collections), or represent a significant distributional disjunction. Most of these are either protected by Florida law (Florida Chapter 5B-40) or are not native to the state (Wunderlin & Hansen 2008). In order to prevent overcollecting, precise locality data for protected taxa have not been included within the specimen citations.

NEW TO FLORIDA

Azolla pinnata R. Br. subsp. **asiatica** R.M.K. Saunders & K. Fowler (Azollaceae). This species, which has a known range of much of the old world tropics (Saunders & Fowler 1992), was reported as new to Florida in the Spring 2008 issue of Wildland Weeds (Brown 2008). Here, we provide voucher information and an infraspecific determination.

Voucher specimens. **Palm Beach Co.:** Loxahatchee River watershed, along a N-S canal, 26° 53' 47.6" N, 80° 8' 37.6" W (NAD 83), Jan 2008 [no day provided], *Bodle s.n.* (USF); unincorporated Jupiter area, canal 1/8 mi W of the intersection of 69th Dr and 149th Pl North, 26° 53' 47.6" N, 80° 8' 37.6" W (NAD 83), 25 Apr 2008, *Bodle s.n.* (FLAS).

Crataegus opaca Hook. & Arn. (Rosaceae). We consider *C. opaca* to be a distinct species and report it here as new to Florida, although it is sometimes placed in synonymy under *Crataegus aestivalis* (Walter) Torr. & A. Gray. It is currently known along the Gulf coast from Texas east to Alabama (USDA, NRCS 2008).

Voucher specimens. **Escambia Co.:** ca. 2 mi SE of South Flomaton, along the Escambia River, at public boat ramp near the Rte 4 bridge, 15 Mar 1981, *Wilhelm 8553* (USF); W bank Escambia River N of Rte Old FL 4 bridge (now removed) S of old concrete boat ramp (via

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Campbell Rd and Boat Ramp Rd), 24 Apr 1994, *Burkhalter 14044* (UWFP); floodplain W side Escambia River N of boat ramp via Mystic Springs Rd, 17 Apr 1988, *Burkhalter 10914* (UWFP). **Santa Rosa Co.:** near E bank Escambia River N of FL 4 bridge, 21 Mar 1985, *Burkhalter 9881* (UWFP); E bank of Escambia River N of FL 184 bridge, 300 ft N of bridge, 23 Oct 1986, *Burkhalter 10472* (UWFP).

Cyperus bipartitus Torr. (Cyperaceae). This is the first report for Florida of this common species of the continental United States and southeast Canada (USDA, NRCS 2008).

Voucher specimen. **Wakulla Co.:** Wakulla River, S of Hwy 98, 13 Sep 2007, *Anderson 23523* (FSU). Species identification was confirmed by Richard Carter (VSC).

Cyperus eragrostis Lam. (Cyperaceae). This collection represents an apparently recent introduction; it was previously known within the southeast United States from South Carolina and Alabama, west to Texas (USDA, NRCS 2008).

Voucher specimen. **Escambia Co.:** corner of Nine Mile Rd and Untreiner Ave, near Pensacola, 28 Oct 2007, *Burkhalter 21650* (UWFP).

Geranium maculatum L. (Geraniaceae). This is the first record for Florida of this common eastern North American plant.

Voucher specimen. **Gadsden Co.:** bottom of steep ravine of Willacoochee Creek drainage, ca. 4.5 air mi NE of Quincy, 14 Apr 2008, *May s.n.* (FSU).

Lamium purpureum L. (Lamiaceae). This represents the first record for Florida of an Eurasian weedy species naturalized throughout much of North America (USDA, NRCS 2008).

Voucher specimens. **Jackson Co.:** mesic calcareous woodland by Day Loop Rd, near NE end of Merritts Mill Pond, 7 Feb 2007, *Anderson 22713* (FSU).

Melochia nodiflora Sw.(Malvaceae). This taxon, with a currently known range of Mexico, Central America, the Caribbean basin and northern South America (Bornstein 1989), is new to the continental United States.

Voucher specimen. **Miami-Dade Co.:** Everglades National Park, "Hole-in-the-Donut" restoration project, 5 Dec 2007, *Sadle 548* (FNPS, USF).

Ochna serrulata (Hochst.) Walp. (Ochnaceae). This commonly cultivated species is native to South Africa and is new to the continental United States. This collection represents the first set of incontrovertibly wild specimens we have seen from Florida, where it has escaped cultivation.

Voucher specimen. **Palm Beach Co.:** High Ridge Scrub Natural Area, N central portion, ca. 500 ft distant from the nearest cultivated area (housing development), T45S, R43E, Sec. 9, 2 Mar 2007, *Lietzky et al. s.n.* (FLAS, USF).

Passiflora vitifolia Kunth (Passifloraceae). This taxon, which is native to Central and South America, is new to the continental United States, where it has escaped cultivation.

Voucher specimen. **Highlands Co.:** spreading rampantly along the shores of Lake August, Placid Lakes Subdivision, Lake Placid, 8 Jul 2008, *Pickert s.n.* (USF).

Sida urens L. (Malvaceae). This is the first report for Florida. It was previously known from the Continental United States only from Alabama (USDA, NRCS 2008). Its known range includes most of the Neotropics and Africa (Fryxell 1988).

Voucher specimen. **Broward Co.:** Long Key Natural Area, 0.5 mi S of Orange Drive on Flamingo Road, ca. 2.5 mi WNW of Cooper City, T50S, R40E, Sec. 23, 26, 16 Jan 2008, *Howell 1048* (USF).

Sphaeropteris cooperi (Hook. ex F. Muell.) R.M. Tryon (Cyatheaceae). This is the first report from Florida for this species and the second for the continental United States. In the United States, it is currently known from Oregon (Wood 2008). It is native to tropical Australia.

Voucher specimen. **Broward Co.:** Tradewinds County Park, N and S of Sample Road, 0.5 mi E of Lyons Road; ca. 3 mi NW of Pompano Beach, T48S, R42E, Sec. 17, 20, 2 Apr 2004, *Howell 779* (USF).

Torilis arvensis (Huds.) Link (Apiaceae). This species was reported for Florida by McGregor (1986), but we have seen no specimens to document its occurrence. This validates its occurrence in the state.

Voucher specimen. **Escambia Co.:** Tarkiln Bayou State Park, SW of Pensacola, 10 May 2008, *Burkhalter 21793* (FSU, UWFP).

SIGNIFICANT NEW COLLECTIONS

Asparagus aethiopicus L.(Asparagaceae). These are the first reports of this Category I species (FLEPPC 2007) for northern Florida and the panhandle. Wunderlin and Hansen (2003) list it for the central and southern peninsula.

Voucher specimens. **Nassau Co.:** inside the St. Marys River inlet, just w of Fort Clinch population stretches for more than 100 m, 17 Nov 2005, *Meisenburg s.n.* (FLAS). **Okaloosa Co.:** South Santa Rosa Island, ca. 0.8 air mi W of Gulf Islands National Seashore, S side of US 98, W side of A5 complex, 30.39719908° N, 86.59745579° W, growing on a coastal dune with *Ilex vomitoria*, *Lantana camara*, and *Elaeagnus pungens*, 4 Jan 2003, *Herring 1643* (USF). **Wakulla Co.:** St. Marks National Wildlife Refuge, naturalized and spreading by old homesite near Wakulla Beach, 27 Jun 2008, *Anderson 23990* (FSU).

Asplenium dentatum L.(Aspleniaceae). This northerly disjunction of this State of Florida endangered species (Florida Chapter 5B-40) is at least 285 km.

Voucher specimen. **Volusia Co.:** Bulow Creek State Park, SSE of the jct. of Walter Boardman Ln and Old Dixie Highway, 20 Feb 2008, *Kunzer et al. 2268* (FLAS, USF).

Asplenium erosum L.(Aspleniaceae). This county record represents a new northern limit for this State of Florida endangered species (Florida Chapter 5B-40).

Voucher specimen. **Flagler Co.:** Bulow Creek State Park, ca. 2.6 km NNW of the jct. of Walter Boardman Ln and Old Dixie Highway, 26 Dec 2008, *Kunzer et al. 2699* (USF).

Brickellia cordifolia Elliott (Asteraceae). These specimens represent a county record and a new locality for a State of Florida endangered species (Florida Chapter 5B-40).

Voucher specimens. **Wakulla Co.:** edge of calcareous woods on N side Hwy 98, 4 Sep 2007, *Anderson 23463* (FSU); N side of US 98, ca. 40 plants at edge of mowed bahiagrass right-of-way against edge of mixed hardwoods, with *Cercis, Carya, Fagus, Prunus serotina,* and *Andropogon*, 19 Sep 2007, *Norris s.n.* (USF).

Bromelia pinguin L. (Bromeliaceae). This is the second county record for Florida; the first, from Hillsborough Co., was in Wunderlin et al. (2002).

Voucher specimen. **Volusia Co.:** Tomoka State Park, between the youth camp and the park concession store, ca. 0.4 km due N of the Old Dixie Highway bridge at the Tomoka River, 29° 20' 43" N, 81° 5' 13" W, 1 Oct 2004, *Kunzer 684* (USF).

Calibrachoa parviflora (Juss.) D'Arcy (Solanaceae). This is the third county record for this species from Florida, all records of which are from panhandle counties.

Voucher specimen. **Escambia Co.:** W Pensacola Beach, Santa Rosa Island, 29 Apr 2007, *Burkhalter 21362* (FSU, UWFP).

Campanula robinsiae Small (Campanulaceae). These collections represent a southern disjunction of over 50 km of this United States and Florida endangered species (Florida Chapter 5B-40) from its only previously known locality in the Chinsegut Hill area of Hernando County, FL.

Voucher specimens. **Hillsborough Co.:** Hillsborough River State Park, bordering a dry edge of a depression marsh, 22 Mar 2006, *vanHoek et al. HR0442* (USF); Hillsborough River State Park, 16 Mar 2007, *Jensen et al. HR0452* (USF).

Casuarina glauca Sieb. ex Spreng. (Casuarinaceae). First reports of this Category I exotic (FLEPPC, 2007) for northern Florida and the Panhandle. Wunderlin and Hansen (2003) list it for the central and southern peninsula.

Voucher specimens. **Franklin Co.:** naturalized (several trees at two sites) on Alligator Point, 21 Jun 2008, *Keys s.n.* (FSU). **St. Johns Co.:** 13th Lane, St. Augustine Beach, planted in yard and spreading to surrounding property near the beach, *Meisenburg s.n.* (FLAS).

Cyperus involucratus Rottb. (Cyperaceae). This is the first report of this exotic species from the Florida panhandle.

Voucher specimens. **Wakulla Co.:** St. Marks National Wildlife Refuge, in woods N edge of Panacea, 27 Sep 2007, *Anderson 23610* (FSU); 3 Jun 2008, *Anderson 23869* (FSU).

Desmodium triflorum (L.) DC. (Fabaceae). This is the first report from west of the Apalachicola River in the panhandle.

Voucher specimen. **Escambia Co.:** lawn of University of West Florida campus, near Pensacola, 5 Nov 2006, *Burkhalter 21256* (FSU, UWFP).

Dyschoriste angusta (A. Gray) Small (Acanthaceae). In Florida, this species had previously been known only from the southern half of the peninsula from southern Polk County southward. The Hernando County specimen is a northwest disjunction of ca. 160 km, and the Wakulla County specimens are a northwest disjunction of ca. 240 km from the Hernando County locality.

Voucher specimens. **Hernando Co.:** Weekiwachee Preserve, ca. 2.4 km W of the jct. of C-595 and US 19, ca. 3.3 km NNW of the junction of the Hernando/Pasco County line with US 19, 28° 38' 58" N, 82° 27' 48" W, 10 Jun 2006, *Kunzer et al. 1824* (USF). **Wakulla Co.:** St. Marks National Wildlife Refuge, grassy roadbed (Rd 203) in coastal wetlands/flatwoods, 8 Sep 2006, *Anderson 22360* (FSU); loamy sand beside Rd 205 just N of Rd 206, 17 May 2007, *Anderson 23060* (FSU); 0.2 mi N of Rd 202 on Rd 205, 6 Jun 2008, *Anderson 23917* (FSU); ecotone between grassy road and tidal marsh at S end of Rd 04, 6 Jun 2008, *Anderson 23924* (FSU).

Eragrostis unioloides (Retz.) Nees ex Steud. (Poaceae). This specimen represents a southern disjunction of at least 130 km from the nearest known population in Polk County, Florida.

Voucher specimen. **Lee Co.:** ca. 6.5 mi E of the jct. of I-75 and Corkscrew Road (C-850), S of Corkscrew Road, 26° 26' 31.2" N, 81° 40'21.3" W, 17 Sep 2005, *Kunzer 1137* (USF).

Ficus aurea Nutt. (Moraceae). This is a new northernmost station for this taxon in Florida.

Voucher specimen. **Volusia Co.:** Ponce Inlet, Lighthouse Point Park, ca. 250 m SE of the lighthouse, 29° 4' 49" N, 80° 55' 30" W, 12 Aug 2005, *Kunzer et al. 1107* (USF).

Hypericum canadense L. (Clusiaceae). This species is new to the central panhandle; it was previously known only from extreme northeast and extreme west Florida.

Voucher specimen. **Calhoun Co.:** locally common amongst grasses and sedges in wet sandy loam bordering ditch along Rte 167 in extreme NW corner of county (Tenmile Creek drainage), 30.54583° N.; 85.36938° W, 18 Aug 2008, *Anderson 24119* (FSU).

Jasminum mesnyi Hance (Oleaceae). This is the first record from the Florida panhandle.

Voucher specimen. **Wakulla Co.:** St. Marks National Wildlife Refuge, naturalized hedge spreading near old shop area, Rd 132, 3 Apr 2008, *Anderson 23743* (FSU).

Juncus bufonius L. (Juncaceae). This collection represents a new southernmost station for this taxon in Florida.

Voucher specimen. **Polk Co.:** Colt Creek State Park, ca. 3.3 km SE of FL 471 bridge over the Withlacoochee River, ca. 4.6 km NE of jct. FL 471 and US 98,28° 17' 13.4" N, 82° 2' 21.1" W, 15 Apr 2008, *Kunzer & Hansen 2391* (USF).

Lepuropetalon spathulatum (Muhl.) Elliott (Parnassiaceae). These are the second and third county records for this State of Florida endangered species (Florida Chapter 5B-40), and all of these are considerably west of its previously known records in Gadsten County.

Voucher specimens. **Escambia Co.:** abundant in ditch near Pensacola Blvd, 29 Mar 2008, *Burkhalter 21744* (FSU, UWFP). **Walton Co.:** ditch beside Hwy, DeFuniak Springs, 15 Mar 2008, *Burkhalter 21720* (FSU, UWFP).

Listera australis Lindl. (Orchidaceae). This easily overlooked species is known sporadically throughout north Florida and the northern Florida peninsula (Wunderlin & Hansen, 2008), and westward to Texas and northward to Quebec, Canada (USDA, NRCS 2008). This station represents the new southern limit for the species, which is threatened in Florida (Florida Chapter 5B-40).

Voucher specimen. **Sarasota Co.:** N of Plantation Boulevard, 14 Jan 2008, *Kunzer 2266* (FLAS, USF).

Mecardonia procumbens (Mill.) Small (Veronicaceae). This specimen represents the first record of this species from the Florida panhandle.

Voucher specimen. **Escambia Co.:** Hwy 29 just S of Church St, near Century, 19 Apr 2008, *Burkhalter 21779* (FSU, UWFP).

Momordica charantia L. (Cucurbitaceae). This is the second report for the panhandle and represents a new county record for the western panhandle. The first record for the panhandle was from Leon County (Anderson 2007).

Voucher specimen. **Escambia Co.:** fence row at corner Gulf St and Jackson St, near Pensacola, 6 Oct 2007, *Burkhalter 21638* (FSU, UWFP).

Peltophorum pterocarpum (DC.) Backer ex K. Heyne (Fabaceae). Previously known from Miami-Dade County and the Monroe County keys, this is the third county record from Florida.

Voucher specimen. **Lee Co.:** South Fort Myers (unincorporated), on the W side of Metro Parkway, ca. 0.4 km SSW of the jct. of Metro Parkway and Colonial Boulevard (FL 884), just E of Tenmile Canal, 81° 51' 11" W 26° 35' 27" N, 29 Sep 2006, *Kunzer 1900* (USF).

Phlebodium aureum (L.) J. Sm. (Polypodiaceae). This is the second county record from the Florida panhandle.

Voucher specimen. **Wakulla Co.:** St. Marks National Wildlife Refuge, fallen palm trunk beside Northline Rd (rd 200), 31 Aug 2006, *Anderson 22310* (FSU).

Polygala verticillata L. var. **isocyta** Fernald (Polygalaceae). This species was previously known in the Florida panhandle from a site reported by Anderson (1986). That population has been extirpated, so these new sites verify its continuance in the county (and the panhandle) in more natural settings.

Voucher specimens. **Wakulla Co.:** St. Marks National Wildlife Refuge, Rd 205 just N of Rd 206, 17 May 2007, *Anderson 23062* (FSU); edge of Rd 108 at junction Rd 107, 17 Jun 2008, *Anderson 23951* (FSU).

Ranunculus pusillus Poir. (Ranunculaceae). These collections, only ca. 25 km apart, represent a southern disjunction of at least 140 km from the nearest known station in Alachua County. (Wunderlin & Hansen 2008).

Voucher specimens. **Hillsborough Co.:** Hillsborough River State Park, bordering a cypress-ringed depression marsh on the S side of the Fort King Trail, ca. 200 yds W of US 301, T27S, R21E, Sec. 17, SE¼ of NW¼, 22 Mar 2006, *vanHoek et al. HR0436* (USF). **Polk Co.:** Colt Creek State Park, ca. 4.8 km SE of FL 471 bridge over the Withlacoochee River, ca. 3.2 km NNE of jct. FL 471 and US 98, 28° 16' 4.1" N, 82° 2' 32.9" W, 3 Apr 2008, *Kunzer et al. 2320* (USF).

Richardia grandiflora (Cham. & Schltdl.) Steud. (Rubiaceae). This species appears to be rapidly spreading throughout peninsular Florida, and the Alachua County specimen represents the current northernmost station in the state.

Voucher specimens. **Alachua Co.:** Gainesville, 2950 Archer Road, weed growing in lawn, 22 Jul 2008, *Weaver 5176* (PIGH, USF). **Volusia Co.:** South Daytona, along the S side of Reed Canal Road, ca. 100 m E of the jct. of Reed Canal Road and Clyde Morris Boulevard, T16S, R33E, Sec. 6, NW¼ of NE¼, 24 Nov 2005, *Kunzer 1221* (USF); along shoulder of Indian Lake Road, next to Volusia County Public Library, ca. 0.5 mi N of US 92, 5 mi W of I-95, T15S, R31E, Sec. 36, 13 Jul 2007, *Slaughter 15741* (USF).

Rumohra adiantiformis (G. Forst.) Ching (Dryopteridaceae). This is the first record from the Florida panhandle.

Voucher specimen. **Franklin Co.:** naturalized under oaks along Bay Street, Apalachicola, 29 Dec 2007, *Anderson 23624* (FSU).

Schefflera arboricola (Hayata) Merr. (Araliaceae). This collection represents a disjunction of over 200 km and a new northern station for this taxon.

Voucher specimen. **Volusia Co.:** Ponce Inlet, Lighthouse Point Park, ca. 250 m SE of the lighthouse, in hammock just upland of coastal swale, 80° 55' 30" W 29° 4' 49" N, 12 Aug 2005, *Kunzer et al. 1108* (USF).

Spigelia loganioides (Torr. & A.Gray ex Endl. & Fenzl) A. DC. (Strychnaceae). The vouchers for this endangered (Florida Chapter 5B-40) endemic species represent an eastern disjunction of at least 85 km from the eastern edge of this species' known range of central Marion County south to north-central Sumter County and west to southern Levy County.

Voucher specimens. **Volusia Co.:** Bulow Creek State Park, 22 Dec 2006, *Kunzer & DuToit 2027* (USF); Bulow Creek State Park, 7 Aug 2008, *Kunzer et al. 2027* (USF).

Spiranthes xitchetuckneensis P.M. Br. (Orchidaceae). This taxon is new to the Florida panhandle.

Voucher specimen. **Wakulla Co.:** St. Marks National Wildlife Refuge, cypress-maple-gum swamp bordering Shepherd's Spring, 13 Nov 2006, *Anderson 22637* (FSU).

Spiranthes lucayana (Britton) Cogn. (Orchidaceae). Endangered in the State of Florida (Florida Chapter 5B-40), this population and county record was first discovered by Charles DuToit, the Park Biologist for the Tomoka Basin Parks State Park complex. Paul Martin Brown has visited this site and confirmed the presence of this species within the park (C. DuToit, pers. comm.).

Voucher specimen. **Volusia Co.:** North Peninsula State Park, 13 Mar 2007, *Kunzer et al. 2078* (USF).

Stachys crenata Raf. (Lamiaceae). This is the only known station outside of Gadsden County for this state endangered taxon (Florida Chapter 5B-40).

Voucher specimen. **Hillsborough Co.:** Hillsborough River State Park, roadside, 2 May 2008, *vanHoek & Parsons 2405* (USF); Hillsborough River State Park, 18 May 2008, *vanHoek & Parsons 2406* (USF).

Tillandsia pruinosa Sw. (Bromeliaceae). This species is endangered in the State of Florida (Florida Chapter 5B-40). In Florida this taxon has only been documented from conservation land in Collier County, with vouchers only being known from the areas of Fakahatchee Strand Preserve State Park and Collier-Seminole State Park. The closer of these, Fakahatchee Strand Preserve State Park, is approximately 60 km to the southeast of this new locality. The collection represents a range extension that is geographically minor but floristically significant.

Voucher specimen. **Lee Co.:** 18 Oct 2007, *Kunzer et al. 2205* (USF).

Tridens carolinianus (Steud.) Henrad (Poaceae). This collection represents a southerly disjunction of over 235 km from the nearest known locality in Suwannee County, FL.

Voucher specimen. **Hillsborough Co.:** "Fishhawk" Preserve, ca. 0.5 mi S of the Alafia River, ca. 0.25 mi N of Fishhawk Boulevard and N of powerline right-of-way, ca. 1 mi E of Bell Shoals, T30S, R21E, Sec. 19, 30 Nov 2006, *Dickman s.n.* (USF).

Urochloa piligera (Muell. ex Benth.) R.D. Webster (Poaceae). This is the first report for this species from Florida west of the Apalachicola River.

Voucher specimen. **Escambia Co.:** along Palafox St near Pensacola, 22 Jul 2007, *Burkhalter 21464* (FSU, UWFP).

Urochloa plantaginea (Link) R.D. Webster (Poaceae). This is the first report for this species from Florida west of the Apalachicola River.

Voucher specimen. **Escambia Co.:** S side Nine Mile Rd near Bowman Ave, near Pensacola, 23 Sep 2006, *Burkhalter 21096* (FSU, UWFP).

Veronica polita Fr. (Veronicaceae). This is the second county of record for this species in Florida, the other being Escambia County.

Voucher specimens. **Leon Co.:** lawn along Robinhood Rd, Tallahassee, 14 May 2008, *Anderson 23817* (FSU); edge of woods on Lakeshore Dr, Tallahassee, 14 May 2008, *Anderson 23819* (FSU).

Xyris longisepala Kral (Xyridaceae). These represent a new county record for this Panhandle endemic species, which is endangered in Florida (Florida Chapter 5B-40).

Voucher specimens. **Wakulla Co.:** St. Marks National Wildlife Refuge, ditch, 26 Jul 2007, *Anderson 23379* (FSU); edge of *Ilex* pond, 4 Sep 2007, *Anderson 23470* (FSU); edge of *Hypericum* zone of pond, 4 Sep 2007, *Anderson 23479* (FSU); cypress pond, 11 Sep 2007, *Anderson 23500* (FSU).

ACKNOWLEDGMENTS

The authors would like to thank Patricia Howell, Stephen Dickman, Carmel vanHoek, Michael Bodle, Jimi Sadle, Richard Weaver, Cecil Slaughter and Lee Norris for the specimens, and Alice Bard (FDEP Florida Park Service), Charles DuToit (FDEP Florida Park Service), and Mary Barnwell (Southwest Florida Water Management District) for the collecting opportunities. Our appreciation is also extended to the personnel at St. Marks National Wildlife Refuge for providing logistical support. We also extend our thanks and appreciation to Kent Perkins (FLAS) and an anonymous reviewer for their helpful comments and suggestions.

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BOOK NOTICES

T.G. Lammers. 2009. **Augustus Green in the Lair of the Pye-a-Saw.** (ISBN none, saddle-stapled). Published by the author. (**Orders:** tlammers@new.rr.com). $5.00 postpaid, 62 pp., illustrated, 8 1/2" × 5 1/2".

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F.O. Zuloaga, O. Morrone, and M.J. Belgrano (eds). 2008. **Catálogo de las Plantas Vasculares del Cono Sur: Argentina, Sur de Brasil, Chile, Paraguay y Uruguay - Volumen 1, 2, and 3.** (ISBN 978-1-930723-70-2, hbk.). Missouri Botanical Garden Press (St. Louis), 4344 Shaw Boulevard, St. Louis, Missouri 63110-2291, U.S.A. (**Orders:** www.mbgpress.org, mbgpress@mobot.org, 314-577-9534, 314-577-9594 fax). $375.00 set, Vol. 1: 984 pp., Vol. 2: 1302 pp., Vol. 3: 1602 pp., 8 1/2" × 11 1/4".

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VASCULAR FLORA OF CHURCHILL RANCH, SARASOTA COUNTY, FLORIDA

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ABSTRACT

Churchill Ranch, owned by Sarasota County, contains 170 hectares with eight plant communities. A survey of vascular plant species conducted from May 2007 to August 2008 yielded 368 taxa, representing 89 families and 241 genera. Of these, 327 (88.9%) were native taxa, 41 (11.1%) exotic, 15 endemic to Florida, four state-endangered, and 29 new county distributional voucher records.

RESUMEN

El Rancho Churchill, propiedad del Sarasota County, contiene 170 hectáreas con ocho comunidades vegetales. Un estudio de las especies de plantas vasculares realizado de Mayo 2007 a Agosto 2008 sumó 368 taxa, de 89 familias y 241 géneros. De estos, 327 (88.9%) fueron nativas, el 41 (11.1%) exóticas, 15 endémicas de Florida, cuatro amenazadas en el estado, y 29 nuevo citadas con testigos en el condado.

INTRODUCTION

Churchill Ranch (CR) is a 170 ha site acquired by Sarasota County through the Environmentally Sensitive Lands Protection Program. The site, situated between Myakka River and Deer Prairie Slough, is managed as part of the nearby Deer Prairie Creek county properties (totaling ca. 3000 ha). It is located about 2.3 km ENE of the junction of Interstate 75 and County Road 777 (River Rd.), approximately 13 km ENE of the gulf coast, 27°07'03"N, 82°19'40"W; T39S, R20E, Sec 5 (Fig. 1). Border Road marks the northern boundary, and Interstate 75 marks the southern boundary of the property. Access to CR is from Border Rd. off Jacaranda Blvd. The results of this research are intended to help Sarasota County make knowledge-based management plans for its property.

SITE OVERVIEW

Geology, Topography, Hydrology, and Soils.—The mean elevation of Churchill Ranch is about 7 m above sea level. The surface soils are mostly acidic, sandy spodosols low in fertility which were deposited by seawater in the Pleistocene during receding sea level. Herein lies the Surficial Aquifer System which contains the water table 2–6 m below mean sea level (FDEP 2007). Below this is the Miocene Hawthorn Group (2–30 m below mean sea level) composed of the Peace River and Arcadia Formations which constitute the Intermediate Aquifer System. Below this is the Florida Aquifer System (100–200 m below mean sea level) which contains the Oligocene Suwannee Limestone, Eocene Ocala Limestone, and Avon Park Formation (Hyde et al. 1991; Halford and Yobbi 2006). The surface soil is 42.7% Eugallie and Myakka fine sands characterized by slash pine (*Pinus elliottii*) flatwoods; Pineda fine sand (21.5%) is largely mesic hammock; Wabasso fine sand (12.7%) is a mixture of mesic hammock and pine flatwoods; Holopan fine sand, (11.6%) occurs in herbaceous marshy depressions. Felda fine sand (7.1%) marks hydric hammocks containing open marshy sites as does Pople fine sand (3.0%). Delray fine sand (1.3%) is found partly in an herbaceous marsh in a hydric hammock as well as a basin marsh which drains into an adjacent pond (USDA 2007).

Climate.—Sarasota County has a subtropical climate with a humid, rainy summer period (June–September) and a cooler, drier period (October–May). The wet season averages 82.07 cm of rainfall and the dry season averages 52.10 cm (SWFWMD 2008) with about 100 days per year receiving precipitation (NCDC 2008). The year 2007 had the lowest amount of annual rainfall for Sarasota County in the last 92 years (SWFWMD 2008). Average wind speed annually is 13 km/hour with prevailing winds usually blowing

J. Bot. Res. Inst. Texas 3(1): 339 – 348. 2009

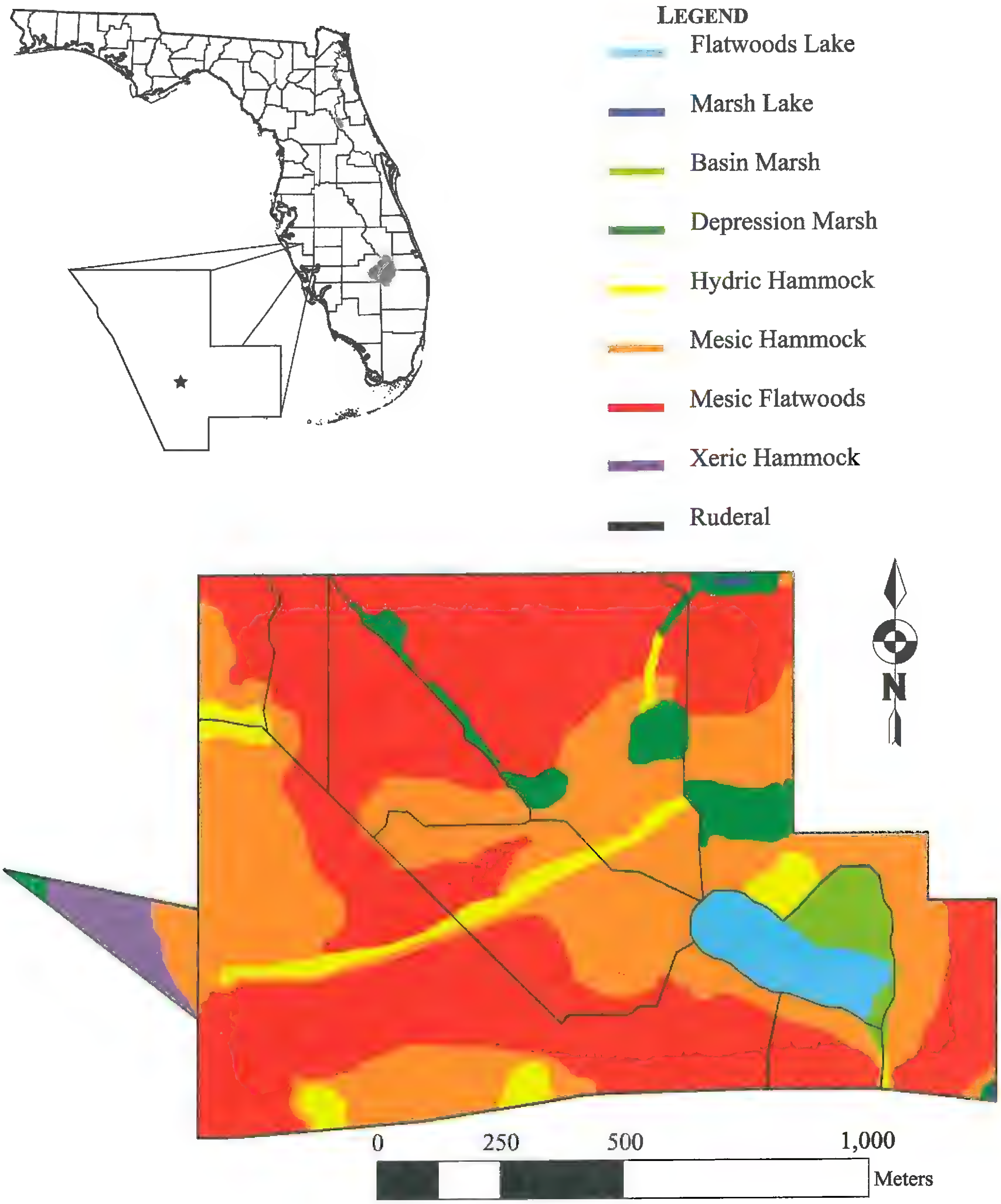

Fig. 1. The location of Churchill Ranch is indicated by the black star within Sarasota County, Florida. The color image shows the habitats within Churchill Ranch.

east. Daily maximum temperatures range from 32.69°C in August to 22.61°C in January. Daily minimum temperatures range from 23.83°C in August to 11.92°C in January. During most years freezing temperatures occur once or twice, only with occasional localized spots of frost. Relative humidity in the morning ranges from 90% in August and 86% in April. Relative humidity in the afternoon ranges from 62% in August to 49% in April. Climate data other than rainfall was averaged from weather stations in Tampa (north of Sarasota) and Ft. Myers (south of Sarasota) as recorded by the NCDC (2008).

Past Land Use.—Aerial photographs from 1948 and 1957 (UF 2004) suggest past logging and the site likely has been cattle ranched for most of the remaining years. Concomitant with this study, intermittently from December 2007 through July 2008, a cattle herd of 10–15 foraged on the land. Significant fire has likely not occurred for 10 or more years.

METHODS

Vascular plant collecting occurred once every 1–4 weeks from May 2007 to August 2008. Permits for endangered species were obtained from the Florida Department of Agriculture and Consumer Services. Voucher specimens were deposited at the University of South Florida herbarium (USF). The nomenclature used follows Wunderlin and Hansen (2003) with updates reflected on the herbarium's website *Atlas of Florida Vascular Plants* (Wunderlin & Hansen 2008). Natural community descriptions follow Florida Natural Areas Inventory (FNAI 1990).

Vascular plants of special interest include those taxa that are state-listed species and exotic species listed by the Florida Exotic Pest Plant Council (FLEPPC 2007). Taxa unreported for Sarasota County as determined by Wunderlin and Hansen (2008) are noted.

RESULTS

The inventory yielded 368 taxa representing 89 families and 241 genera at Churchill Ranch. Native species comprised 327 taxa (88.9%) and 41 (11.1%) were exotic species. The greatest numbers of taxa recorded were in the families Poaceae (59), Asteraceae (51), Cyperaceae (39), Fabaceae (18), Rubiaceae (11), Euphorbiaceae (9), and Plantaginaceae (9). *Rhynchospora*, with 10 taxa, represented the largest genus, followed by *Cyperus* (8), *Hypericum* (7), *Quercus* (7), *Panicum* (7), *Andropogon* (6), *Dichanthelium* 6), *Fimbristylis* (6), *Tillandsia* (6), *Eragrostis* (5), and *Polygala* (5). The families containing the most number of exotics were the Poaceae (13), Fabaceae (6), Asteraceae (4), and Amaranthaceae (3). Of the exotics, eight were listed as category I and three as category II invasive plant species as designated by the Florida Exotic Pest Plant Council (FLEPPC 2007) (Table 1). There were 29 new county records for Sarasota. Fifteen species (3.58%) are endemic to Florida, of which three are in the family Campanulaceae. Four endangered species, *Glandularia tampensis*, *Lythrum flagellare*, *Tillandisa fasciculata*, and *T. utriculata*, and two commercially exploited species, *Encyclia tampensis* and *Osmunda regalis* var. *spectabilis*, were found. One hybrid, *Quercus laurifolia* × *Q. pumila*, was documented.

PLANT COMMUNITIES

The classification for plant communities found within the study (Fig. 1) following the Florida Natural Areas Inventory (FNAI 1990) is discussed below from the lowest elevation to the highest followed by ruderal areas.

Flatwoods Lake.—One large pond covering 4.9 ha (2.9%) of the site is dominated by *Typha domingensis* with other herbs such as *Eleocharis interstincta* and *Hydrocotyle umbellata* growing along its perimeter. A small island sits in the center, dominated by *Polygonum glabrum* and *Salix caroliniana*. It is accessible by land when the water level is down.

Marsh Lake.—Marsh lakes characterize the other perennial bodies of water at the site, covering 0.2 ha (<0.01%). In the extreme southeast corner a small pool of water next to Interstate 75 reaches into the site. This contains the floating aquatics *Lemna valdiviana* and *Wolfiella oblonga*. Also along Border Rd. lies a small elliptic pond where the native species *Azolla carolinensis* and *Nuphar advena*, and the exotics, *Ludwigia peruviana*, *Panicum repens*, and *Salvinia minima*, are found. During the peak of the drought, this pond was nearly dry.

Basin Marsh.—A basin marsh occurs directly adjacent to the large pond, covering 3.3 ha (1.9%). The ground is densely covered with herbs such as *Iris hexagona*, *Phyla nodiflora*, and *Polygonum punctatum*. Before the summer rains of 2008, *Baccharis halimifolia* had successfully invaded and reached maturity. However after the rains, the inundated conditions began to cause dieback of these shrubs.

Table 1. Exotic invasive plant species at CR found on FLEPPC's list (2007).

Category I	Category II
Dioscorea bulbifera	*Ricinus communis*
Hymenachne amplexicaulis	*Sphagneticola trilobata*
Ludwigia peruviana	*Urena lobata*
Melinis repens	
Panicum repens	
Schinus terebinthifolia	
Solanum viarum	

Depression Marsh.—Depression marshes occur on 15.1 ha (8.9%) of the site. From the beginning of the study and through the spring of 2008, the soils were relatively dry and never inundated. However, significant summer rain in 2008 saturated and flooded these marshes. *Hypericum fasciculatum* dominated one marsh. Other marshes are characterized by herbaceous species such as *Lythrum flagellare* and *Phyla nodiflora*. Others are dominated by *Cephalanthus occidentalis* and *Salix caroliniana* and include the exotic *Hymenachne amplexicaulis*.

Hydric Hammock.—The hydric hammocks occur on 15.5 ha (9.1%) of the site. The dominant canopy trees are *Quercus laurifolia* and *Q. virginiana* with *Ulmus americana* as an occasional associate. An isolated patch of hydric hammock is dominated by *Fraxinus caroliniana*. Various, predominantly herbaceous, marshy sites occur here. Associations include *Kosteletzkya pentacarpos–Ipomoea sagittata*, *Lobelia feayana–Sisyrinchium angustifolium*, *Cladium jamaicense–Hibiscus grandiflorus*, and *Helianthus agrestis–Campanula floridana*. Epiphytes such as *Encyclia tampensis*, *Tillandsia* spp., *Vittaria lineata*, and *Pleopeltis polypodioides* var. *michauxiana* are abundant. The exotic *Solanum viarum* also occurs here.

Mesic Hammock.—The mesic hammocks occur on 57.9 ha (34.1%) of the site with *Quercus virginiana* dominating the canopy and *Sabal palmetto* the subcanopy. *Serenoa repens* characterizes the understory, interspersed with *Callicarpa americana* and *Smilax bona-nox*. Exotic species include *Schinus terebinthifolia*, which is being treated for removal by the county, and *Sphagneticola trilobata*.

Mesic Flatwoods.—The mesic flatwoods is the dominant community, covering 69.7 ha (41.0%). The canopy consists mainly of *Pinus elliottii* with a dense understory of *Serenoa repens* of 1–2m, reaching 3–4m in a few places. The dense nature of the flatwoods is obviously due to fire suppression. Other common elements include the shrubs *Asimina reticulata*, *Ilex glabra*, *Lyonia fruticosa*, *Lyonia lucida*, *Quercus elliottii*, *Quercus minima*, and *Vaccinium darrowii* and the vines *Galactia elliottii* and *Smilax auriculata*. Common herbaceous species include *Aristida spiciformis*, *Fimbristylis puberula*, *Ludwigia maritima*, *Lygodesmia aphylla*, *Panicum anceps*, *Polygala setacea*, *Pteridium aquilinum* var. *pseudocaudatum*, and *Solidago odora* var. *chapmanii*.

Xeric Hammock.—A small ridge of land in the westernmost portion, wedged between a mesic hammock and a marsh, represents a xeric hammock of 1.7 ha (1.0%). Here the canopy is composed of *Quercus nigra* and *Quercus virginiana*. The understory has mostly *Serenoa repens* but its sparseness here allows open sites to occur. In these open areas plants such as *Gratiola hispida*, *Opuntia humifusa*, *Pityopsis graminifolia*, and *Stipulicida setacea* var. *lacerata* occur.

Ruderal.—The ruderal areas are found along the roads, trails, and firebreaks which make up about 1.7 ha (1.0%). Patches of vegetation along the roads and trails are seasonally mowed. Common in these areas are the native species *Bulbostylis stenophylla*, *Paspalum setaceum*, and *Setaria parviflora*. Common exotics are *Commelina diffusa*, *Fimbristylis schoenoides*, and *Paspalum notatum* var. *saurae*.

DISCUSSION

Disturbance, mainly fire, is a well-recognized component of Florida ecosystems. At Churchill Ranch, fire suppression has allowed the flatwoods to become thickly overgrown with woody vegetation. Other disturbances which significantly impact the plant communities include foraging by domestic cattle, feral pigs, and anthropogenic mechanical disturbance (mowing, roller chopping).

Mowing has an essential role in maintaining paths and firebreaks. However, mowing maintains herbaceous communities as disturbed sites and may favor weedy, short life cycle, high-fecundity species such as the exotics *Digitaria longiflora* and *Eragrostis atrovirens* and the native *Paspalum setaceum*. It also may replace the effects of grazing allowing the exotic *Paspalum notatum* var. *saurae* to continue. These disturbed sites may also serve as corridors for the spread of invasive species.

Roller chopping has been implemented as a way to reduce shrub vegetation, mainly *Serenoa repens* as well as *Lyonia* spp. and *Quercus* spp., to reduce fire intensity, and to increase light and resource availability to understory herbs. Approximately 50 hectares of mesic flatwoods adjacent to Interstate 75 were roller chopped at Churchill Ranch in March 2007, reducing fire hazard to drivers on the interstate. *Serenoa repens* was predominantly affected with some saplings such as *Pinus elliottii* toppled as well. A thick layer of detritus from affected plants, uncommon in flatwoods, was also left. As the roller chopping occurred near the end of this study post-treatment effects were not assessed. Roller chopping without burning at a dry prairie in nearby Myakka River State Park did not increase the abundance of native grasses (Watts et al. 2006).

Huffman (2006) estimates that most pine flatwoods have historically experienced natural fire, not started by man, at least every five years. The lack of fire disturbance, or fire suppression, may have negatively impacted the species richness of Churchill Ranch in plants as well as other organisms. Burning would be ideal for this site but is problematic due to its location next to Interstate 75.

Exotic disturbances (cattle grazing and feral hogs) and the lack of natural disturbance (fire) have likely played a large role in the ecology of CR. Plant herbivory by large animals has been intensive at CR and could have quickly reduced or extirpated some taxa. Many taxa recorded at CR seemed to occur as one delicate, reduced population. Some examples include species found exclusively along fencerows along the property boundary such as *Muhlenbergia capillaris*, *Nephrolepis exaltata*, *Osmunda regalis*, and *Thelypteris kunthii*.

ANNOTATED LIST OF VASCULAR PLANTS

The list is artificially grouped into PTERIDOPHYTES, GYMNOSPERMS, MONOCOTS, and DICOTS. Within these four groups, families are listed alphabetically, and within each family, the taxa are alphabetical by genus and species. Following each species name is its authorship, habitat in the study area, and the senior author's collection number. The habitat abbreviations are **FL**–flatwoods lake, **ML**–marsh lake, **BM**–basin marsh, **DM**–depression marsh, **HH**–hydric hammock, **MH**–mesic hammock, **MF**–mesic flatwoods, **XH**–xeric hammock, and **RU**–ruderal areas. Annotations preceding taxa are ^ for a new county record, * for exotic species, and + for taxa endemic to the state of Florida.

PTERIDOPHYTES

Azollaceae
Azolla filiculoides Lam.—ML; *403*

Blechnaceae
Blechnum serrulatum Rich.—MF; *279*
Woodwardia virginica (L.) Sm.—MF; *280*

Dennstaedtiaceae
Pteridium aquilinum (L.) Kuhn var. *pseudocaudatum* (Clute) Clute ex A. Heller—MF; *397*

Nephrolepidaceae
Nephrolepis exaltata (L.) Schott—MH; *444*

Osmundaceae
Osmunda regalis L. var. *spectabilis* (Willd.) A. Gray—MH; *445*

Polypodiaceae
Phlebodium aureum (L.) J. Sm.—HH; *214*
Pleopeltis polypodioides (L.) E.G. Andrews & Windham var. *michauxiana* (Weath.) E.G. Andrews & Windham—MH; *199*

Salviniaceae
**Salvinia minima* Baker—ML; *668*

Thelypteridaceae
Thelypteris kunthii (Desv.) C.V. Morton—MH; *631*

Vittariaceae
Vittaria lineata (L.) Sm.—HH; *227*

GYMNOSPERMS

Pinaceae
Pinus elliottii Engelm.—MF; *217*

MONOCOTS

Alismataceae
Sagittaria graminea Michx.—DM; *824*
Sagittaria lancifolia L.—DM; *264*

Amaryllidaceae
Crinum americanum L.—HH; *327*

Araceae
^*Lemna valdiviana* Phil.—ML; *404*
Pistia stratiotes L.—ML; *402*
^*Wolfiella oblonga* (Phil.) Hegelm.—ML; *405*

Arecaceae
Sabal palmetto (Walter) Lodd. ex Schult. & Schult. f.—MH; *662*
Serenoa repens (W. Bartram) Small—MF; *100*

Bromeliaceae
Tillandsia balbisiana Schult. & Schult. f.—MH; *635*
Tillandsia fasciculata Sw.—MH; *374*
Tillandsia recurvata (L.) L.—MH; *361*
Tillandsia setacea Sw.—MH; *323*
Tillandsia usneoides (L.) L.—MH; *111*
Tillandsia utriculata L.—XH; *252*

Commelinaceae
**Commelina diffusa* Burm. f.—RU; *152*
Commelina erecta L.—XH; *157*
**Murdannia nudiflora* (L.) Brenan—RU; *394*

Cyperaceae
Bulbostylis ciliatifolia (Elliott) Fernald—XH; *313*
Bulbostylis stenophylla (Elliott) C.B. Clarke—RU; *257*
Carex lupuliformis Sartwell ex Dewey—ML; *190*
+*Carex vexans* F.J. Herm.—FL; *209*
Cladium jamaicense Crantz—HH; *144*
Cyperus compressus L.—RU; *333*
^*Cyperus croceus* Vahl—RU; *228*
Cyperus distinctus Steud.—BM; *270*
Cyperus ligularis L.—RU; *350*
Cyperus odoratus L.—BM; *191*
Cyperus polystachyos Rottb.—DM; *124, 349*
Cyperus retrorsus Chapm.—MF; *314*
Cyperus surinamensis Rottb.—BM; *255*
Eleocharis geniculata (L.) Roem. & Schult.—FL; *452*
Eleocharis interstincta (Vahl) Roem. & Schult.—FL; *197*
Fimbristylis autumnalis (L.) Roem. & Schult.—FL; *211*
Fimbristylis cymosa R. Br.—RU; *150*
^*Fimbristylis dichotoma* (L.) Vahl—RU; *345*
Fimbristylis puberula (Michx.) Vahl—MF; *712*
**Fimbristylis schoenoides* (Retz.) Vahl—RU; *443*
Fimbristylis spadicea (L.) Vahl—HH; *218*
Fuirena breviseta (Coville) Coville—RU; *454*
Fuirena scirpoidea Michx.—RU; *204, 654*
^*Kyllinga odorata* Vahl—RU; *337*
^*Lipocarpha micrantha* (Vahl) G.C. Tucker—MH; *384*
^**Oxycaryum cubense* (Poepp. & Kunth) Palla—ML; *369*
Rhynchospora colorata (L.) H. Pfeiff.—MH; *666*
Rhynchospora divergens Chapm. ex M.A. Curtis—MF; *371*
Rhynchospora fascicularis (Michx.) Vahl—MF; *205*
^*Rhynchospora fernaldii* Gale—MF; *358*
Rhynchospora globularis (Chapm.) Small—HH; *419*
Rhynchospora inundata (Oakes) Fernald—DM; *363*
Rhynchospora microcarpa Baldwin ex A. Gray—MH; *268, 419*
Rhynchospora nitens (Vahl) A. Gray—ML; *413*
^*Rhynchospora odorata* C. Wright ex Griseb—BM; *230*
Rhynchospora plumosa Elliott—MF; *267*
Schoenoplectus tabernaemontani (C.C. Gmel) Palla—BM; *193*
Scleria reticularis Michx.—RU; *412*
Scleria triglomerata Michx.—XH; *253, 428*

Dioscoreaceae
**Dioscorea bulbifera* L.—RU; *296*

Eriocaulaceae
Eriocaulon decangulare L.—ML; *275*
Lachnocaulon anceps (Walter) Morong—MF; *123*
Syngonanthus flavidulus (Michx.) Ruhland—MF; *115*

Haemodoraceae
Lachnanthes caroliana (Lam.) Dandy—MF; *379*

Hypoxidaceae
Hypoxis curtissii Rose—MH; *224*
Hypoxis juncea Sm.—MF; *225*

Iridaceae
Iris hexagona Walter—BM; *602*
Sisyrinchium angustifolium Mill.—HH; *498*

Juncaceae
Juncus effusus L. subsp. *solutus* (Fernald & Wiegand) Hämet-Ahti—BM; *174*
Juncus marginatus Rostk.—DM; *206*
Juncus megacephalus M.A. Curtis—DM; *781*
Juncus scirpoides Lam.—MF; *435*

Marantaceae
Thalia geniculata L.—BM; *401*

Orchidaceae
Encyclia tampensis (Lindl.) Small—HH; *212*
Habenaria floribunda Lindl.—MH; *489*

Poaceae
Androgogon glomeratus (Walter) Britton et al. var. *glaucopsis* (Elliott) C. Mohr—MF; *659*
Andropogon glomeratus (Walter) Britton et al. var. *pumilus* (Vasey) Vasey ex L.H. Dewey—MF; *331*
^*Andropogon longiberbis* Hack.—RU; *286*
Andropogon ternarius Michx.—MF; *447*
^*Andropogon virginicus* L. var. *glaucus* Hack.—MF; *424*
Andropogon virgincus L. var. *virginicus*—MF; *441*
Aristida patula Chapm. ex Nash—HH; *342*
Aristida purpurascens Poir. var. *tenuispica* (Hitchc.) Allred—MF; *431*
Aristida spiciformis Elliott—MF; *355*
Axonopus fissifolius (Raddi) Kuhlm.—HH; *289*
Axonopus furcatus (Flüggé) Hitchc.—HH; *166*
Cenchrus spinifex Cav.—RU; *303*
**Cynodon dactylon* (L.) Pers.—RU; *202*
**Dactyloctenium aegyptium* (L.) Willd. ex Asch. & Schweinf.—RU; *340*
^*Dichanthelium aciculare* (Desv. ex Poir.) Gould & C.A. Clark—XH; *461*
Dichanthelium commutatum (Schult.) Gould—MH; *222*
Dichanthelium dichotomum (L.) Gould—MF; *364*
Dichanthelium ensifolium (Baldwin ex Elliott) Gould—MH; *347*
Dichanthelium erectifolium (Nash) Gould & C.A. Clark—MF; *441*
Dichanthelium laxiflorum (Lam.) Gould—MH; *169*

Digitaria ciliaris (Retz.) Koeler—RU; *287*
**Digitaria longiflora* (Retz.) Pers.—RU; *288*
Echinochloa muricata (P. Beauv.) Fernald—BM; *186*
+*Echinochloa paludigena* Wiegand—HH; *466*
Echinochloa walteri (Pursh) A. Heller—DM; *192*
**Eleusine indica* (L.) Gaertn.—RU; *326*
**Eragrostis atrovirens* (Desf.) Trin. ex Steud.—RU; *330*
^**Eragrostis bahiensis* (All.) Vignolo ex Janch.—RU; *219*
Eragrostis hypnoides (Lam.) Britton et al.—DM; *128*
Eragrostis spectabilis (Pursh) Steud.—MH; *223,449*
Eragrostis virginica (Zuccagni) Steud.—RU; *655*
**Eremechloa ophiuroides* (Munro) Hack.—RU; *271*
Eustachys glauca Chapm.—HH; *229*
Eustachys petraea (Sw.) Desv.—RU; *302*
**Hymenachne amplexicaulis* (Rudge) Nees—DM; *362*
**Melinis repens* (Willd.) Zizka—RU; *300*
Muhlenbergia capillaris (Lam.) Trin.—MH; *453*
^*Oplismenus hirtellus* (L.) P. Beauv.—HH; *390*
Panicum anceps Michx.—MF; *396*
Panicum dichotomiflorum Michx. var. *bartowense* (Scribn. & Merr.) Fernald—BM; *414*
Panicum hemitomon Schult.—ML; *185*
Panicum hians Elliott—RU; *285*
**Panicum repens* L.—ML; *184*
^*Panicum tenerum* Beyr. ex Trin.—MF; *408*
Panicum virgatum L.—MF; *318*
^*Paspalum conjugatum* P. J. Bergius—MF; *410, 459*
Paspalum floridanum Michx.—HH; *231*
**Paspalum notatum* Flüggé var. *saurae* Parodi—RU; *237*
Paspalum setaceum Michx.—RU; *208*
^*Reimarochloa oligostachya* (Munro ex Benth.) Hitchc.—DM; *272, 458*
Saccharum giganteum (Walter) Pers.—DM; *407, 434*
Sacciolepis striata (L.) Nash—BM; *210*
Schizachyrium scoparium (Michx.) Nash—MF; *370, 432*
Setaria parviflora (Poir.) Kerguélen—RU; *339, 382*
Sorghastrum secundum (Elliott) Nash—MF; *425*
Sporobolus domingensis (Trin.) Kunth—MF; *433*
**Sporobolus indicus* (L.) R. Br. var. *pyramidalis* (P. Beauv.) Veldkamp—RU; *665*
Tripsacum dactyloides (L.) L.—HH; *663*
^**Urochloa distachya* (L.) T.Q. Nguyen—RU; *376*

Pontederiaceae
Pontederia cordata L.—ML; *660*

Smilacaceae
Smilax auriculata Walter—MF; *416*
Smilax bona-nox L.—MH; *805*

Typhaceae
Typha domingensis Pers.—FL; *101*
Typha latifolia L.—BM; *194*

Xyridaceae
Xyris caroliniana Walter—MF; *306*
Xyris elliottii Chapm.—MF; *114, 269*

DICOTS

Acanthaceae
Dyschoriste oblongifolia (Michx.) Kuntze—MH; *265*
+*Justicia angusta* (Chapm.) Small—DM; *130*
^*Stenandrium dulce* (Cav.) Nees—MH; *196*

Adoxaceae
Viburnum obovatum Walter—MH; *664*

Amaranthaceae
**Alternanthera sessilis* (L.) R. Br. ex DC.—HH; *622*
**Chenopodium ambrosioides* L.—RU; *360*
**Gomphrena serrata* L.—RU; *336*

Anacardiaceae
Rhus copallinum L.—MF; *317*
**Schinus terebinthifolia* Raddi—MH; *175*
Toxicodendron radicans (L.) Kuntze—MH; *142*

Annonaceae
+*Asimina reticulata* Shuttlew. ex Chapm.—MF; *611*

Apiaceae
Eryngium baldwinii Spreng.—HH; *107*
Ptilimnium capillaceum (Michx.) Raf.—DM; *179*

Apocynaceae
Asclepias pedicellata Walter—MF; *261*
Asclepias perennis Walter—HH; *129*

Aquifoliaceae
Ilex cassine L.—HH; *319, 492*
Ilex glabra (L.) A. Gray—MF; *122*

Araliaceae
Centella asiatica (L.) Urb.—FL; *442*
Hydrocotyle umbellata L.—FL; *200*

Asteraceae
^*Acmella oppositifolia* (Lam.) R.K. Jansen var. *repens* (Walter) R.K. Jansen—HH; *620*
Ambrosia artemisiifolia L.—RU; *290*
^*Baccharis glomeruliflora* Pers.—MH; *479*
Baccharis halimifolia L.—BM; *464*
Bidens alba (L.) DC.—RU; *242*
Boltonia diffusa Elliott—ML; *281*
+*Carphephorus odoratissimus* (J.F. Gmel.) H. Hebert var. *subtropicanus* (DeLaney et al.) Wunderlin & B.F. Hansen—MF; *430*
Chrysopsis mariana (L.) Elliott—HH; *470*
Cirsium horridulum Michx.—MH; *234*
Cirsium nuttallii DC.—MH; *137, 170*
^*Conoclinium coelestinum* (L.) DC.—MH; *143*
Conyza canadensis (L.) Cronquist—RU; *338*
+*Coreopsis leavenworthii* Torr. & A. Gray—DM; *134*
Elephantopus elatus Bertol.—MF; *301*
**Emilia fosbergii* Nicolson—RU; *484*
**Emilia sonchifolia* (L.) DC.—RU; *707*
Erechtites hieraciifolius (L.) Raf. ex DC.—MH; *235*
Erigeron quercifolius Poir.—MH; *247*
Erigeron vernus (L.) Torr. & A. Gray—MH; *346*

Eupatorium capillifolium (Lam.) Small ex Porter & Britton—MH; *463*
Eupatorium mohrii Greene—MF; *278*
Eupatorium rotundifolium L.—MF; *451*
Euthamia caroliniana (L.) Greene ex Porter & Britton—MF; *429*
Gamochaeta pensylvanica (Willd.) Cabrera—MH; *251*
Helenium amarum (Raf.) H. Rock—RU; *164*
Helianthus agrestis Pollard—HH; *309*
Heterotheca subaxillaris (Lam.) Britton & Rusby—RU; *809*
Hieracium megacephalon Nash—XH; *256*
^*Iva microcephala* Nutt.—DM; *353*
Lygodesmia aphylla (Nutt.) DC.—MF; *618*
Melanthera nivea (L.) Small—HH; *329, 709*
Mikania cordifolia (L. f.) Willd.—MF; *483*
Mikania scandens (L.) Willd.—MH; *202*
^*Pectis glaucescens* (Cass.) D.J. Keil—RU; *307*
+*Pectis linearifolia* Urb.—RU; *366*
Pectis prostrata Cav.—RU; *368*
Pityopsis graminfolia (Michx.) Nutt.—XH; *321*
Pluchea baccharis (Mill.) Pruski—HH; *246*
Pluchea odorata (L.) Cass.—HH; *145*
Pseudognaphalium obtusifolium (L.) Hilliard & B.L. Burtt—MH; *487*
Pterocaulon pycnostachyum (Michx.) Elliott—MH; *118*
Sericocarpus tortifolius (Michx.) Nees—MF; *393*
Solidago odora Aiton var. *chapmanii* (A. Gray) Cronquist—MF; *273*
Solidago stricta Aiton—MH; *481*
Sphagneticola trilobata (L.) Pruski—MH; *348* (preceded by *)
Symphyotrichum bahamense (Britton) G.L. Nesom—HH; *480*
Symphyotrichum carolinianum (Walter) Wunderlin & B.F. Hansen—HH; *480*
Symphyotrichum dumosum (L.) G.L. Nesom—HH; *478*
**Tridax procumbens* L.—RU; *806*
Verbesina virginica L.—HH; *420*
Vernonia blodgettii Small—MH; *244*

Bignoniaceae
Campsis radicans (L.) Seemann—HH; *388*

Boraginaceae
Heliotropium polyphyllum Lehm.—MF; *409*

Brassicaceae
Rorippa teres (Michx.) Stuckey—HH; *603*

Cactaceae
Opuntia humifusa (Raf.) Raf.—XH; *328*

Campanulaceae
+*Campanula floridana* S. Watson ex A. Gray—HH; *621*
+*Lobelia feayana* A. Gray—HH; *496*
+*Lobelia homophylla* E. Wimm.—MH; *139*

Caryophyllaceae
Drymaria cordata (L.) Willd. ex Schult.—MH; *299*
+*Stipulicida setacea* Michx. var. *lacerata* C.W. James—XH; *332*

Chrysobalanaceae
Licania michauxii Prance—XH; *138*

Cistaceae
Helianthemum corymbosum Michx.—XH; *165*
Lechea torreyi (Chapm.) Legg. ex Britton—MH; *471*

Clusiaceae
Hypericum cistifolium Lam.—MH; *220*
Hypericum fasciculatum Lam.—DM; *112*
Hypericum gentianoides (L.) Britton et al.—MH; *154*
Hypericum hypericoides (L.) Crantz—MH; *245*
Hypericum mutilum L.—DM; *181*
Hypericum tenuifolium Pursh—MF; *105*
Hypericum tetrapetalum Lam.—MH; *710*

Convolvulaceae
Dichondra carolinensis Michx.—MH; *493*
Ipomoea cordatotriloba Dennst.—RU; *398*
Ipomoea pandurata (L.) G. Mey—HH; *633*
Ipomoea sagittata Poir.—HH; *284*

Cornaceae
Cornus foemina Mill.—HH; *248*

Cucurbitaceae
Melothria pendula L.—HH; *310*

Ebenaceae
Diospyros virginiana L.—MH; *708*

Ericaceae
Bejaria racemosa Vent.—MF; *195*
Lyonia fruticosa (Michx.) G.S. Torr.—MF; *104*
Lyonia lucida (Lam.) K. Koch—MF; *119*
Vaccinium arboreum Marshall—MH; *158*
Vaccinium darrowii Camp—MF; *262*
Vaccinium stamineum L.—MF; *106*

Euphorbiaceae
Acalypha gracilens A. Gray—MH; *213*
Chamaesyce hyssopifolia (L.) Small—RU; *241*
Chamaesyce maculata (L.) Small—RU; *667*
Cnidoscolus stimulosus (Michx.) Engelm. & A. Gray—XH; *136*
Croton glandulosus L.—MH; *334*
Croton michauxii G.L. Webster—MF; *203*
**Phyllanthus tenellus* Roxb.—MH; *488*
**Ricinus communis* L.—RU; *297*
Stillingia sylvatica L.—MF; *108*

Fabaceae
Amorpha herbacea Walter—XH; *160*
Centrosema virginianum (L.) Benth.—XH; *254*
Chamaecrista fasciculata (Michx.) Greene—MF; *159*
Crotalaria rotundifolia J.F. Gmel.—RU; *110*
**Crotalaria spectabilis* Roth—RU; *612*
Dalea carnea (Michx.) Poir.—MF; *808*
**Desmodium incanum* DC.—RU; *260*
**Desmodium triflorum* (L.) DC.—RU; *377*
Galactia elliottii Nutt.—MF; *162*
Galactia regularis (L.) Britton et al.—MH; *163*
Indigofera caroliniana Mill.—MF; *249*
**Macroptilium lathyroides* (L.) Urb.—RU; *446*
**Medicago lupulina* L.—RU; *499*
^*Mimosa strigillosa* Torr. & A. Gray—RU; *147*
**Senna obtusifolia* (L.) H.S. Irwin & Barneby—RU; *146*

Sesbania herbacea (Mill.) McVaugh—BM; *341*
^*Sesbania vesicaria* (Jacq.) Elliott—DM; *462*
Vicia acutifolia Elliott—HH; *601*

Fagaceae
Quercus laurifolia Michx.—HH; *325*
Quercus minima (Sarg.) Small—MF; *103, 392*
Quercus myrtifolia Willd.—MF; *469*
Quercus nigra L.—XH; *380*
Quercus pumila Walter—MF; *634*
Quercus virginiana Mill.—MH; *375*
^*Quercus laurifolia* x *Q. pumila*—MF; *426, 711*

Gentianaceae
Sabatia brevifolia Raf.—MF; *365*
Sabatia grandiflora (A. Gray) Small—FL; *236*

Hydroleaceae
Hydrolea corymbosa J. Macbr. ex Elliott—ML; *298*

Lamiaceae
Callicarpa americana L.—MH; *140*
Hyptis alata (Raf.) Shinners—HH; *315*
Piloblephis rigida (W. Bartram ex Benth.) Raf.—MF; *421*
Salvia lyrata L.—MH; *121*
Scutellaria integrifolia L.—MF; *810*
Teucrium canadense L.—RU; *258*
Trichostema dichotomum L.—MH; *151*

Lauraceae
Cassytha filiformis L.—MH; *266*
Persea palustris (Raf.) Sarg.—HH; *418*

Loganiaceae
Mitreola petiolata (J.F. Gmel.) Torr. & A. Gray—HH; *226*

Lythraceae
+*Lythrum flagellare* Shuttlew. ex Chapm.—DM; *117, 615*

Malvaceae
Hibiscus grandiflorus Michx.—HH; *282*
Kosteletzkya pentacarpos (L.) Ledeb—HH; *283*
^**Melochia corchorifolia* L.—MH; *316*
Sida ulmifolia Mill.—RU; *438*
**Urena lobata* L.—MH; *221*

Melastomataceae
Rhexia mariana L.—DM; *661*

Myricaceae
Myrica cerifera L.—MF; *216*

Nymphaeaceae
Nuphar advena (Aiton) Aiton—ML; *274*

Oleaceae
Fraxinus caroliniana Mill.—HH; *605*

Onagraceae
Gaura angustifolia Michx.—RU; *240*
Ludwigia maritima R.M. Harper—MF; *259, 455*
**Ludwigia peruviana* (L.) H. Hara—ML; *657*
^*Ludwigia repens* J.R. Forst.—DM; *171, 423*
Ludwigia suffruticosa Walter—MF; *170*

Orobanchaceae
Buchnera americana L.—MF; *131*

Oxalidaceae
Oxalis corniculata L.—RU; *153*

Phytolaccaceae
Phytolacca americana L.—RU; *312*

Plantaginaceae
Bacopa monnieri (L.) Pennell—DM; *177*
Gratiola hispida (Benth. ex Lindl.) Pollard—RU; *155*
Gratiola pilosa Michx.—XH; *624*
Linaria canadensis (L.) Chaz.—MF; *494*
**Lindernia crustacea* (L.) F. Muell.—RU; *350*
Lindernia grandiflora Nutt.—DM; *180*
Mecardonia acuminata (Walter) Small var. *peninsularis* (Pennell) Rossow—MF; *188*
+*Micranthemum glomeratum* (Chapm.) Shinners—HH; *385*
Scoparia dulcis L.—MF; *250*

Polygalaceae
Polygala incarnata L.—MF; *440*
Polygala lutea L.—MF; *277*
Polygala nana (Michx.) DC.—MF; *610*
Polygala setacea Michx.—MF; *276*
Polygala violacea Aubl.—RU; *109*

Polygonaceae
+*Polygonella polygama* (Vent.) Engelm. & A. Gray var. *brachystachya* (Meisn.) Wunderlin—MF; *161*
Polygonum glabrum Willd.—FL; *198*
Polygonum punctatum Elliott—DM; BM; *176*

Rosaceae
Rubus trivialis Michx.—RU; *495*

Rubiaceae
Cephalanthus occidentalis L.—DM; *183*
Diodia teres Walter—RU; *243*
Diodia virginiana L.—DM; *178, 383*
Galium tinctorium L.—FL; *600*
Houstonia procumbens (J.F. Gmel.) Standl—HH; *437*
Mitchella repens L.—XH; *607*
**Oldenlandia corymbosa* L.—RU; *357*
Oldenlandia uniflora L.—MF; *417*
Psychotria sulzneri Small—MH; *215*
**Richardia brasiliensis* Gomes—RU; *356*
Spermacoce remota Lam.—MH; *156, 395*

Salicaceae
Salix caroliniana Michx.—DM; HH; *491, 653*

Samolaceae
Samolus valerandi L. subsp. *parviflorus* (Raf.) Hultén—DM; *116*

Sapindaceae
Acer rubrum L.—MF; *389*

Sapotaceae
Sideroxylon reclinatum Michx.—MF; *187*

Solanaceae
Physalis arenicola Kearney—XH; *320*

Physalis pubescens L.—HH; *629*
Solanum americanum Mill.—RU; *351*
**Solanum viarum* Dunal—HH; *623*

Tetrachondraceae
Polypremum procumbens L.—RU; *113*

Ulmaceae
Ulmus americana L.—HH; *387*

Urticaceae
Boehmeria cylindrica (L.) Sw.—DM; *263*
Parietaria floridana Nutt.—HH; *604*

Verbenaceae
+*Glandularia tampensis* (Nash) Small—HH; *632*
Phyla nodiflora (L.) Greene—DM; *120*
Verbena scabra Vahl—HH; *141*

Violaceae
Viola sororia Willd.—MH; *497*

Viscaceae
Phoradendron leucarpum (Raf.) Reveal & M.C. Johnst.—MF; *381*

Vitaceae
Ampelopsis arborea (L.) Koehne—MF; *172*
Parthenocissus quinquefolia (L.) Planch.—MF; *352*
Vitis aestivalis Michx.—MH; *343*
Vitis rotundifolia Michx.—MF; *135*
Vitis shuttleworthii House—HH; *201*

ACKNOWLEDGMENTS

We thank Bruce F. Hansen and John M. Kunzer for their invaluable assistance with identification. We would also like to thank Bruce F. Hansen and two anonymous reviewers for their comments on the manuscript, and Kathleen Hotchkiss for her help with graphics. We thank the Land Manager, Debbie Blanco, of Sarasota County, for access to the site. The senior author thanks his wife for her company on some of his collecting trips.

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VASCULAR FLORA OF A SALINE PRAIRIE IN WINN PARISH, LOUISIANA

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ABSTRACT

We describe the vascular flora of a saline prairie in Winn Parish, Louisiana. The prairie contains 59 species of which three are federal and/or state rare. While saline prairies are a distinct and rare community, they show certain similarities to other West Gulf Coastal Plain plant communities, notably sandstone outcrops and barrens.

RESUMEN

Se describe la flora vascular de una pradera salina en Winn Parish, Louisiana. La pradera contiene 59 especies de las que tres son raras en el estado. Mientras que las praderas salinas son una comunidad diferente y rara, muestras ciertas semejanzas con otras comunidades vegetales de la llanura costera del West Gulf, notablemente afloramientos de areniscas y tierras yermas.

INTRODUCTION

Recent research on saline prairies in Louisiana has greatly expanded our knowledge of this community (Reid et al. in prep). This community occurs in central and northwestern Louisiana, eastern Texas, and southern Arkansas (McInnis et al. 1993; Keith et al. 2004; Lester et al. 2005; Arkansas Natural Heritage Commission 2006; Diggs et al. 2006; Reid et al. in prep). In pre-settlement times, saline prairies were probably uncommon. The estimate for Louisiana is fewer than 800 ha with only 10 to 25 percent remaining (Lester et al. 2005). Because of many factors, including urban sprawl, agriculture, grazing, oil exploration, off-road vehicle activity, and agro-forestry, this community has been badly degraded and greatly reduced in extent and is now ranked globally imperiled (G1)(Lester et al. 2005).

The earliest described saline prairies in Louisiana are several in Winn Parish (McInnis et al.1993; Lester et al. 2005). Interest in the Winn Parish saline prairies initially focused on the federally-listed *Geocarpon minimum*, which had not previously been found in Louisiana (McInnis et al. 1993).

A renewed interest in saline prairies since 2005 (MacRoberts et al. 2007; Reid et al. 2007; Reid et al. in prep) and in *Geocarpon minimum* (MacRoberts & MacRoberts 2007, 2008) led to an interest in the floristic and edaphic conditions of the Winn Parish saline prairies, which had not previously been thoroughly described (McInnis et al. 1993).

In this paper we describe the floristics of Upper Weyerhaeuser Prairie (aka Castor Creek Saline Prairie [McInnis et al. 1993]), one of the Winn Parish saline prairies.

General edaphic and community information regarding saline prairies including Upper Weyerhaeuser Prairie as well as an extensive bibliography of this community and its rare species is given in Reid et al. (in prep).

STUDY SITE AND METHODS

Figure 1 is an aerial view of Upper Weyerhaeuser Prairie (T10NR1ES2). Figure 2 is a scenic view of the prairie. The prairie measures approximately 3.9 ha. A road runs through its center with shallow ditches along its sides. We excluded the road and the ditches from the survey. We also avoided prairie edges, staying at least three meters from the edge. Upper Weyerhaeuser Prairie, unlike many other saline prairies, has no mima

J. Bot. Res. Inst. Texas 3(1): 349 – 354. 2009

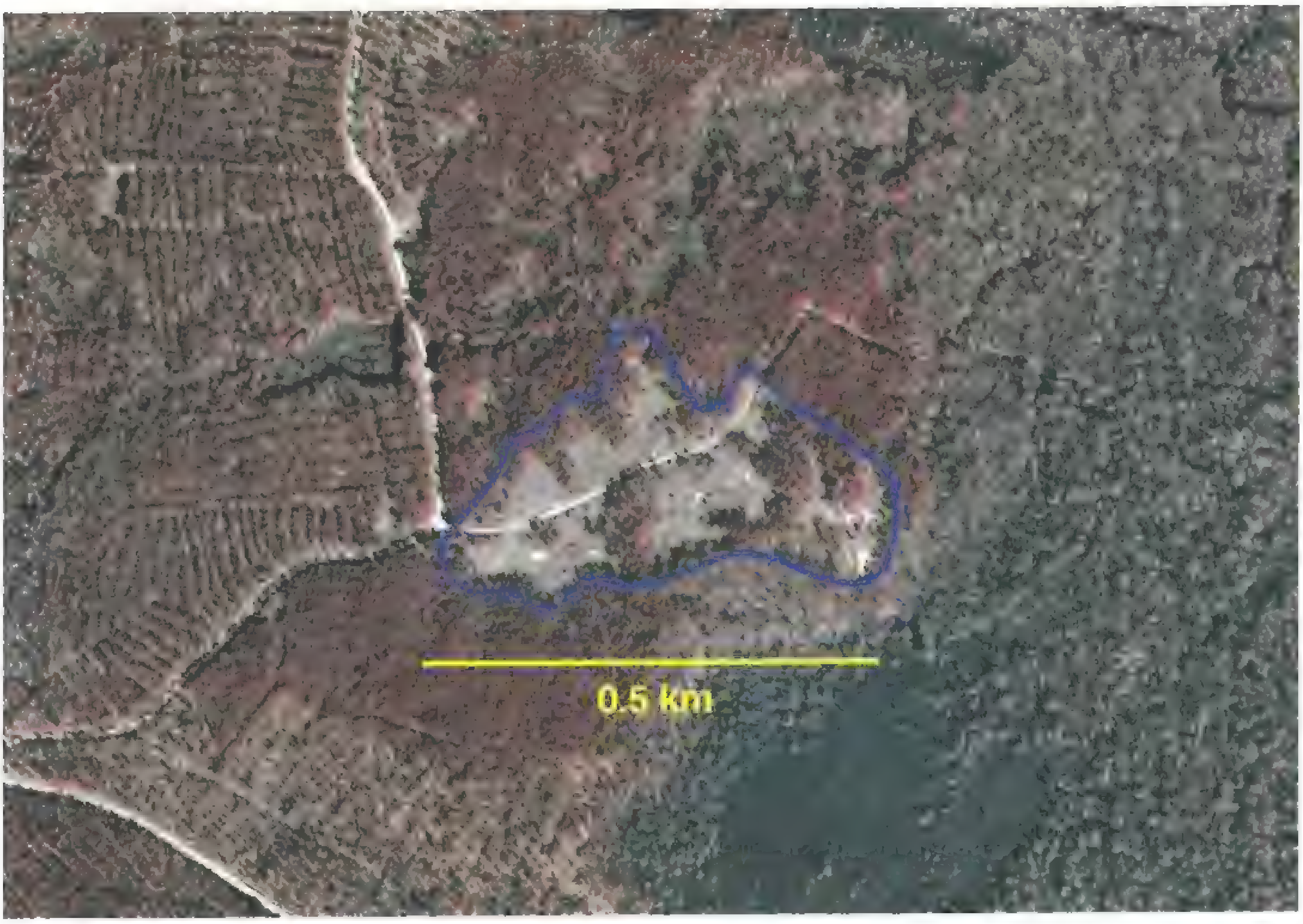

Fig. 1. Aerial view of Upper Weyerhaeuser Prairie.

(pimple) mounds or wet depressions. The soils are classified as Brimstone fine-silty, siliceous, thermic Glossic Natraqualfs. They are high in sodium and are alkaline. They resist wetting, inducing droughty conditions. Prairie substrait has physical properties similar to a dense clay hardpan that is resistant to root penetration (McInnis et al. 1993; Boyd et al. 1998; Reid et al. in prep.). Two lichens, *Cladonia caroliniana* (Schwein.) Tuck. and *Cladonia sobolescens* Nyl. ex Vain., are a common ground cover in some areas of the prairie (Fig. 3). The surrounding forest is dominated by *Pinus taeda*, *Quercus stellata*, *Quercus phellos*, *Ilex vomitoria*, *Crataegus spathulata*, and *Vaccinium* spp., with *Chasmanthium laxum* being the dominant understory species.

Upper Weyerhaeuser Prairie as a whole was collected monthly between 19 March and 5 November 2008. Specimens are deposited at the Louisiana State University Herbarium (LSU) and Louisiana State University in Shreveport Herbarium (LSUS). Nomenclature follows USDA NRCS (2008), Diggs et al. (2006), and *Flora of North America* (1993–2006).

In order to investigate species richness, two 0.1 ha plots each with two nested 0.001 ha plots and two nested 0.0001 ha plots were established within the prairie. All species in the plots were recorded.

RESULTS

Table 1 lists the vascular species found in Upper Weyerhaeuser Prairie. All collection numbers refer to B.R. MacRoberts and M.H. MacRoberts. An asterisk * indicates an exotic species. Table 2 summarizes the plot data.

Upper Weyerhaeuser Prairie had 59 species. The two 0.1 ha plots had a mean of 50 species (range 47 to 53), the four 0.001 ha plots had a mean of 19.5 species (range 15 to 28) and the four 0.0001 ha plots had a mean of 16.5 species (range 9 to 26). Only one exotic species was found in the prairie.

Fig. 2. View across Upper Weyerhaeuser Prairie.

Fig. 3. Lichens in Upper Weyerhaeuser Prairie.

DISCUSSION

Rare species at Upper Weyerhaeuser Prairie include *Geocarpon minimum* (G2S2), *Schoenolirion wrightii* (G3S2), and *Phemeranthus parviflorus* (G5S3) (Louisiana Natural Heritage Program 2008). *Geocarpon minimum* was first discovered at this prairie in 1991 when approximately 620 plants were found in four locations (unpublished field notes on file with the Louisiana Natural Heritage Program). Fewer plants were observed in 1992, but the survey was less intensive. Surveys in 2007 and 2008 discovered the species at only one location. Total number of plants was not determined but four 0.0001 ha plots had 141 and 357 plants in those two years, respectively (MacRoberts & MacRoberts 2007, 2008). *Geocarpon minimum* is now known from Caddo, DeSoto, and Winn parishes in Louisiana (MacRoberts & MacRoberts 2007, 2008). The presence of *Schoenolirion wrightii* in Upper Weyerhaeuser Prairie adds Winn Parish to the list of Caddo, Red River, Natchitoches, De Soto parishes where it had previously been found (MacRoberts & MacRoberts 1993; Louisiana Natural Heritage Program 2008). In Louisiana, *Phemeranthus parviflorus* is known from Caddo, De Soto, Natchitoches, Red River, Sabine, and Winn parishes (Louisiana Natural Heritage Program 2008). Both *Schoenolirion wrightii* and *Phemeranthus parviflorus* are known from both saline prairies and sandstone outcrops in Louisiana (MacRoberts & MacRoberts 1993; Louisiana Natural Heritage Program 2008); whereas *Geocarpon minimum* is known only from saline prairies.

Upper Weyerhaeuser Prairie is relatively uniform. The two 0.1 ha plots contained all of the species found in the prairie although the plots constituted only about five percent of the prairie. Further, it was clear from repeatedly walking the entire prairie that virtually the same species occurred throughout.

Compared with saline prairies in northwestern Louisiana (Reid et al. in prep.), Upper Weyerhaeuser prairie is relatively depauperate. It lacks mima mounds and wet depressions and thus plant species associated with them. But also it lacks many other species found in the northwestern Louisiana saline prairies such as *Cooperia drummondii, Evax verna, Gratiola flava, Lechea san-sabeana, Marshallia caespitosa, Minuartia drummondii, Minuartia muscorum, Opuntia humifusa, Phacelia glabra,* and *Saxifraga texana* (Reid et al. in prep.).

Nonetheless, floristically Upper Weyerhaeuser Prairie most resembles the northwestern Louisiana saline prairies in De Soto and Caddo parishes (Reid et al. in prep.). We found that approximately 69 percent of the Upper Weyerhaeuser flora occurred in them. Upper Weyerhaeuser next most resembles sandstone outcrop communities on the Kisatchie Ranger District of the Kisatchie National Forest in Natchitoches Parish, Louisiana, with approximately 50 percent of its flora occurring in them (MacRoberts & MacRoberts 1993). Species in common between them include *Bigelowia nuttallii, Evolvulus sericeus, Phemeranthus parviflorus, Polygala verticillata,* and *Schoenolirion wrightii*. Next in community resemblance is Black Branch Barrens on the Angelina National Forest in Jasper County, Texas, which has just below 50 percent of the Upper Weyerhaeuser flora (Marietta & Nixon 1983; Orzell 1990; MacRoberts et al. 1997). Interesting plants in common between Black Branch Barrens and Upper Weyerhaeuser Prairie are *Bigelowia nuttallii, Evolvulus sericeus, Phemeranthus parviflorus,* and *Schoenolirion wrightii*.

ACKNOWLEDGMENTS

This work was partly supported by contract CFM663087, Louisiana Department of Wildlife and Fisheries. Alan Boyd, Land Use Forester, at Weyerhaeuser Company, aided with the research. Shirley Tucker identified the lichens. Charles Allen made several valuable comments on the paper.

TABLE 1. Species of Upper Weyerhaeuser Saline Prairie.

Acanthaceae
Ruellia humilis Nutt., 8254
Alliaceae
Allium canadense L., 8160, 8167
Asteraceae
Bigelowia nuttallii L.C. Anderson, 8313
Coreopsis tinctoria Nutt., 8166
Helenium flexuosum Raf., 8253
Iva angustifolia Nutt. ex DC., 8331
Krigia dandelion Nutt., 8154
Krigia occidentalis Nutt., 8129
Liatris pycnostachya Michx., 8314, 8326, 8329
Senecio tomentosus Michx., 8125
Solidago nitida Torr & A. Gray, 8307, 8330
Symphyotrichum dumosum (L.) Nesom, 8362
Brassicaceae
Lepidium densiflorum Schrad., 8168
Campanulaceae
Triodanis perfoliata L., 8158
Caryophyllaceae
Geocarpon minimum Mack., (no specimen collected).
Cistaceae
Lechea tenuifolia Michx., 8251
Clusiaceae
Hypericum drummondii (Greve. & Hook.) T.&G., 8243, 8311
Convolvulaceae
Evolvulus sericeus Sw., 8153, 8244
Cyperaceae
Carex complanata Torr. & Hook., 8166, 8169
Fimbristylis puberula (Michx.) Vahl, 8163, 8246
Rhynchospora globularis (Chapm.) Small, 8240, 8150, 8252
Rhynchospora pusilla Chapm. ex M.A. Curtis, 8241
Droseraceae
Drosera brevifolia Pursh, 8135
Ericaceae
Vaccinium arboreum Marshall, 8308
Euphorbiaceae
Croton wildenowii G.L. Webster, 8310, 8332
Fabaceae
Neptunia lutea (Leavenw.) Benth., 8250
Gentianaceae
Sabatia campestris Nutt., 8242
Hyacinthaceae
Schoenolirion wrightii Sherman, 8172, 8131
Hypoxidaceae
Hypoxis rigida Chapm., 8156
Iridaceae
**Sisyrinchium rosulatum* Bicknell, 8161
Sisyrinchium sagittiferum Bicknell, 8164
Lamiaceae
Hedeoma hispida Pursh, 8165, 8247
Liliaceae
Nothoscordum bivalve (L.) Britt., 8132
Linaceae
Linum medium (Planch.) Britton, 8255
Onagraceae
Oenothera linifolia Nutt., 8155
Orchidaceae
Spiranthes vernalis Engelm & A. Gray, 8249
Oxalidaceae
Oxalis corniculata L., 8134
Pinaceae
Pinus taeda L., 8126
Plantaginaceae
Plantago pusilla Nutt., 8133
Plantago virginica L., 8157
Poaceae
Agrostis elliottiana Schult., 8149, 8162
Aristida longespica Poir., 8365, 8382
Aristida oligantha Michx., 8369, 8381
Dichanthelium dichotomum (L.) Gould, 8170
Dichanthelium sphaerocarpon (Ell.) Gould, 8171, 8248
Eragrostis hirsuta (Michx.) Nees, 8322, 8360
Eragrostis refracta (Muhl.) Scribn., 8323, 8333, 8361, 8364
Paspalum setaceum Michx., 8363
Schizachyrium scoparium (Michx.) Nash, 8371
Tridens strictus (Nutt.) Nash, 8366, 8368, 8383
Polygalaceae
Polygala mariana Mill., 8239
Polygala verticillata L., 8245
Portulacaceae
Phemeranthus parviflorus (Nutt.) Kiger, 8309
Rosaceae
Crataegus marshallii Egglest., 8173, 8174
Rubiaceae
Diodia teres Walter, 8312
Houstonia micrantha (Shinners) Terrell, 8127
Houstonia pusilla Schoepf, 8130
Sapotaceae
Sideroxylon lanuginosum Michx., 8151
Scrophulariaceae
Agalinis tenuifolia (Vahl) Raf., 8367, 8370

Table 2. Species richness in Upper Weyerhaeuser Prairie.

Plot and plot size (ha)	No. of plots	Average species (range)
Plot A		
0.0001	2	20.0(14–26)
0.001	2	22.5(17–28)
0.1	1	53.0
Plot B		
0.0001	2	13.0(9–17)
0.001	2	16.5(15–18)
0.1	1	47.0

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VASCULAR FLORA OF MORSE CLAY PRAIRIES IN NORTHWESTERN LOUISIANA

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ABSTRACT

We describe the floristics, soils, small-scale species richness, and phytogeographic affinities of Morse Clay calcareous prairies in northwestern Louisiana. Four 0.1 ha plots had 159 species and averaged 85 species, eight 0.001 ha plots averaged 27 species, and eight 0.0001 ha plots averaged 19.5 species. The most diverse families were Asteraceae (40 species), Fabaceae (23 species), and Poaceae (17 species). The soils are predominantly alkaline high-calcium silty clay loams. The North American distribution of Morse Clay prairie species is eastern and central. Whether Morse Clay prairies should be considered a distinct community type will depend on further research on isolated prairies in nearby Texas, Arkansas, and Louisiana, but at the present time they do not appear to be distinct from at least some of the calcareous prairies in the region.

RESUMEN

Se describe la florística, suelos, riqueza de especies a pequeña escala, y afinidades fitogeográficas de las praderas calcáreas de Morse Clay en el noroeste de Louisiana. Cuatro parcelas 0.1 ha tuvieron 159 especies y una media de 85 especies, ocho parcelas de 0.001 ha tuvieron una media de 27 especies, y ocho parcelas de 0.0001 ha tuvieron una media de 19.5 especies. Las familias con más diversidad fueron Asteraceae (40 especies), Fabaceae (23 especies), y Poaceae (17 especies). Los suelos son predominantemente margas limosas alcalinas con alto contenido en calcio. La distribución norteamericana de las especies de pradera de los Morse Clay es oriental y central. Si las praderas Morse Clay deben, o no, considerarse un tipo de comunidad diferente dependerá de investigaciones posteriores en praderas asiladas en las cercanas Texas, Arkansas, y Louisiana, pero actualmente no parecen ser diferentes de al menos algunas praderas calcáreas de la región.

INTRODUCTION

While prairies are one of the most endangered plant communities in North America, they are one of the best studied (Sims & Risser 2000; Diggs et al. 2006). Thousands of books and papers have been written on the floristics, management, and restoration of prairies. Louisiana prairies were documented in the eighteenth and nineteenth centuries by land surveyors, cartographers, and explorers; however, botanists did not begin to study them until the 1930s (Brown 1997; MacRoberts et al. 1997, 2003; MacRoberts & MacRoberts 2004 and references therein). Southeastern prairies, except for the prairie belt of Alabama and Mississippi, have been woefully neglected in the literature (Leidolf & McDaniel 1998; Peacock & Schauwecker 2003; Barone 2005; Barone & Hill 2007). However, such isolated prairies were extensive in pre-European times, and there still exist many small, relatively natural prairies in the pineywoods region of Texas, Arkansas, Louisiana, and Mississippi (Jordan 1973; Brown et al. 2002; Foti et al. 2003; Zollner et al. 2003; MacRoberts & MacRoberts 2004).

Included in this group are the "Morse Clay" prairies of northwestern Louisiana and southwestern Arkansas (McInnis 1997; Lester et al. 2005; Arkansas Natural Heritage Commission pers. comm.). These are small, grassy openings that occur on reddish, fine textured, alkaline and calcareous clays and silt loams (Chaffin et al. 1959). While the fire frequency was not different from surrounding woodland, these prairies, like so many others, are maintained as openings in the oak-pine woodlands by soil-dependent variations in grass biomass, resulting differences in fire intensity, and extreme soil properties (Diggs & Schulze 2003; Lester et al. 2005; Diggs et al. 2006). Herbivory by large mammals may also play a role.

The purpose of this paper is to describe the floristics of Morse Clay prairies in northwestern Louisiana and to compare them with prairies elsewhere in the southeast.

THE SETTING

Morse Clay prairies and soils occur on Pleistocene intermediate terraces in northwestern and central Louisiana and southwestern Arkansas. Prairies typically exist as small openings on side-slopes and flats in shortleaf pine/oak-hickory forests (Figs. 1 and 2) (Lester et al. 2005). Presettlement extent of Morse Clay prairies is estimated to have been between 800 and 4,000 ha, with 5 to10 percent thought to remain (Louisiana Natural Heritage Program 1993). A recent status survey of Louisiana Morse Clay prairies revealed 11 occurrences totaling a mere 60 ha, and nearly half of that area was in poor condition (MacRoberts & MacRoberts 2007b).

The best known examples of Morse Clay prairies are found on the 9,000 ha Barksdale Air Force Base and 14,000 ha Bodcau Wildlife Management Area in Bossier Parish, Louisiana. Barksdale AFB was purchased in the late 1930s. The western side is maintained as an air force base; the eastern side is undeveloped and supports undulating oak-pine woodlands with occasional prairie openings. Prior to its establishment as an air base, large scale timber harvesting had eliminated all virgin timber. When the Federal Government acquired the land, it was generally open fields and cropland (McInnis 1997). Current management of the eastern part is focused on wildlife, oil and gas exploitation, timber harvesting, and recreation. Consequently, few areas remain in natural or semi-natural condition. All of the prairie area has been subject to disturbance, notably fire suppression, food plot development with plowing, and part of it was at one time a bombing range with large craters. Teague and Wendt (1994) and McInnis (1997) give an overview of the entire area.

Bodcau WMA, owned by the U.S. Army Corps of Engineers and leased by the Louisiana Department of Wildlife and Fisheries, has similar habitat to that of Barksdale AFB with similar areas of Morse Clay prairie (Lester et al. 2005). At Bodcau by the mid-1950s, prairies were cotton farmed and over-grazed by livestock (John Haygood, pers. comm.). Some of the prairie area in Bodcau WMA is protected in registered natural areas, but much of the area that was historically prairie is now plowed land managed for food plots. All areas where Morse Clay prairie occurs have had ground disturbance in the past.

METHODS

In order to have comparable samples, we modified the plot design of Peet et al. (1998) used widely in the southeast. We established four study plots in four prairies away from prairie edges (Fig. 3). Three plots were established in closely adjacent prairies on Barksdale AFB, and one plot was established on a single prairie on Bodcau WMA 32 km to the northeast. Each plot measured 20 m × 50 m or 31.6 m × 31.6 m (0.1 ha). Within each 0.1 ha plot were two nested 3.16 m × 3.16 m (0.001 ha) plots. Each of these in turn had a 1 m × 1 m (0.0001 ha) nested plot within it. Thus, there were four 0.1 ha plots, eight 0.001 ha plots, and eight 0.0001 ha plots. We surveyed each plot for total species. All species in the plots were recorded every month over a year between 2006 and 2008 (except in mid-winter). A specimen of all species collected is deposited at Louisiana State University Herbarium (LSU). Nomenclature follows Kartesz and Meacham (2005) and *Flora of North America* (1993–2006).

Using our list of species found in the four Morse Clay prairies and data from *Flora of North America* (1993–2006) and NatureServe (2008), we plotted the North American distribution of species by state, region, or province to determine the geographic pattern of Morse Clay prairie species (Fig. 4).

We collected soil samples from the upper 20 cm within the prairies, in the woodlands above the prairies, and in the woodlands below them at about 3 meters from the prairie edge. These we had analyzed for pH, various elements, and soil texture at Louisiana State University Soil Testing and Plant Analysis Laboratory.

We made brief floristic surveys of other Morse Clay prairies in Caddo and Bossier parishes (MacRoberts & MacRoberts 2007b).

RESULTS/DISCUSSION

The four study plots had 159 species: North Pond had 105, Lower Green Tree had 85, Bomb Crater had 75, and Nemastylis had 76 (Table 1). Asteraceae, Fabaceae, and Poaceae dominated with 40, 23, and 17 species, respectively. The plot richness (Table 2) is about average for open plant communities (e.g., bogs and xeric

sandylands) throughout the West Gulf Coastal Plain with about 20 species per 0.0001 ha, 27 species per 0.001 ha, and 85 species per 0.1 ha) (MacRoberts et al. 2007). Table 3 gives Sorenson's Index of Similarity among the four prairies. This level of similarity indicates that they are the same community. Soil texture in the prairies was either silty clay loam or silty clay (Table 4). Soil textures of upslope woodlands ranged from silty clay loam to very fine sandy loam. The range of pH value in the prairies was 6.8 to 8.3, n = 7. By contrast, pH values ranged from 4.6 to 5.6, n = 4 in the woods above the prairie, and 5.2 to 7.4, n = 3 in the woods below prairies. Calcium concentration was substantially higher in prairie soils versus soils collected from adjacent woodlands. Potassium concentration also seems to generally be higher in prairie soils.

We found five state rare species in the prairies. *Carex meadii* (S2S3) is found in several west Louisiana parishes where it occurs in calcareous and coastal prairies and in sandstone glades. It occurred in or near all of the study plots. *Coreopsis palmata* Nutt. (S1), found only in Bossier and Claiborne parishes, occurred only in Bomb Crater Prairie, and only at its upper edge. At Bomb Crater, *Coreopsis palmata* appeared to be associated mainly with upland woodlands. *Houstonia purpurea* var. *calycosa* (S2) occurs in Bossier, Caldwell, Grant, LaSalle, and Winn parishes in calcareous prairies. This species was common in North Pond Prairie but was not found at the other Morse Clay prairies. *Nemastylis geminiflora* (S2S3) is found in several West Gulf Coastal Plain parishes. It was found in the Lower Green Tree and Nemastylis prairie plots and in the prairies adjacent to both the North Pond and the Bomb Crater prairie plots. *Koeleria macrantha* Ledeb. (S1) (Reid 5546 LSU) occurred in Bomb Crater Prairie but just outside of the plot. This is one of the only two extant populations in Louisiana, the other being in a calcareous prairie in Winn Parish. Further information on rare species and the explanation of "S" ranks can be found in Louisiana Natural Heritage Program (2007).

Isolated prairies occur across the West Gulf Coastal Plain and eastward (Peacock & Schauwecker 2003; MacRoberts & MacRoberts 2004). While few prairies have been the subject of comprehensive floristic studies, enough have been done to provide quantitative comparisons. Brown et al. (2002) studied Windham Prairie in Polk County, Texas, 250 km southwest of Bossier Parish. An Index of Similarity (Sorenson's) between Windham Prairie and our Morse Clay prairies is 37. Leidolf and McDaniel (1998) studied Sixteen Section Prairie in Oktibbeha County, Mississippi, about 450 km east of Bossier Parish. An Index of Similarity between it and our Morse Clay prairies is also 37. Barone and Hill (2007) studied several blackland prairies in Alabama and Mississippi about 500 km east of our study sites. An Index of Similarity between those sites and the Morse Clay prairies is 31. Contrasted with these figures, the Keiffer prairies in Winn Parish, Louisiana (Smith et al. 1989; MacRoberts & MacRoberts 1996), 125 km southeast of the Morse Clay prairies, have an Index of Similarity of 51 with the Morse Clay prairies. This figure is especially interesting since North Pond Prairie on the Bodcau WMA, only 32 km northeast of the three Barksdale AFB prairies, differed from them as much as did the Keiffer prairies (Table 3). Unfortunately, there are no complete floristic inventories of the blackland and Morse Clay prairies of southwestern Arkansas. However, Foti (1989) provides a preliminary list of species in ten of the less disturbed blackland prairies approximately 120 km north of our Morse Clay prairies. An Index of Similarity between those sites and our Morse Clay prairies is 44 a difference that indicates the importance of additional study of southwestern Arkansas prairies, notably since such species as *Carex microdonta* Torr. & Hook. and *Spiranthes magnicamporum* C. Sheviak have recently been found in them (Theo Witsell pers. comm.).

Morse clay soils proved similar to soils of other calcareous prairies in Louisiana, Arkansas, and Texas which are alkaline and are high in calcium. Of the properties tested for all prairies, phosphorus and potassium were the same; only magnesium was higher (MacRoberts & MacRoberts 1996, 2004).

Judging habitat condition is difficult, notably when there is no known "natural" habitat for comparison. Unfortunately, this is the case for Morse Clay prairies, none of which are pristine; all have been subject to various unnatural disturbances, notably clearing, grazing, plowing, fire suppression, and bombing. One can only attempt to reconstruct what these prairies were like by studying those surviving remnants that most closely resemble our best estimate of the structure and composition of presettlement plant communities.

Fig. 1. Morse Clay Prairie.

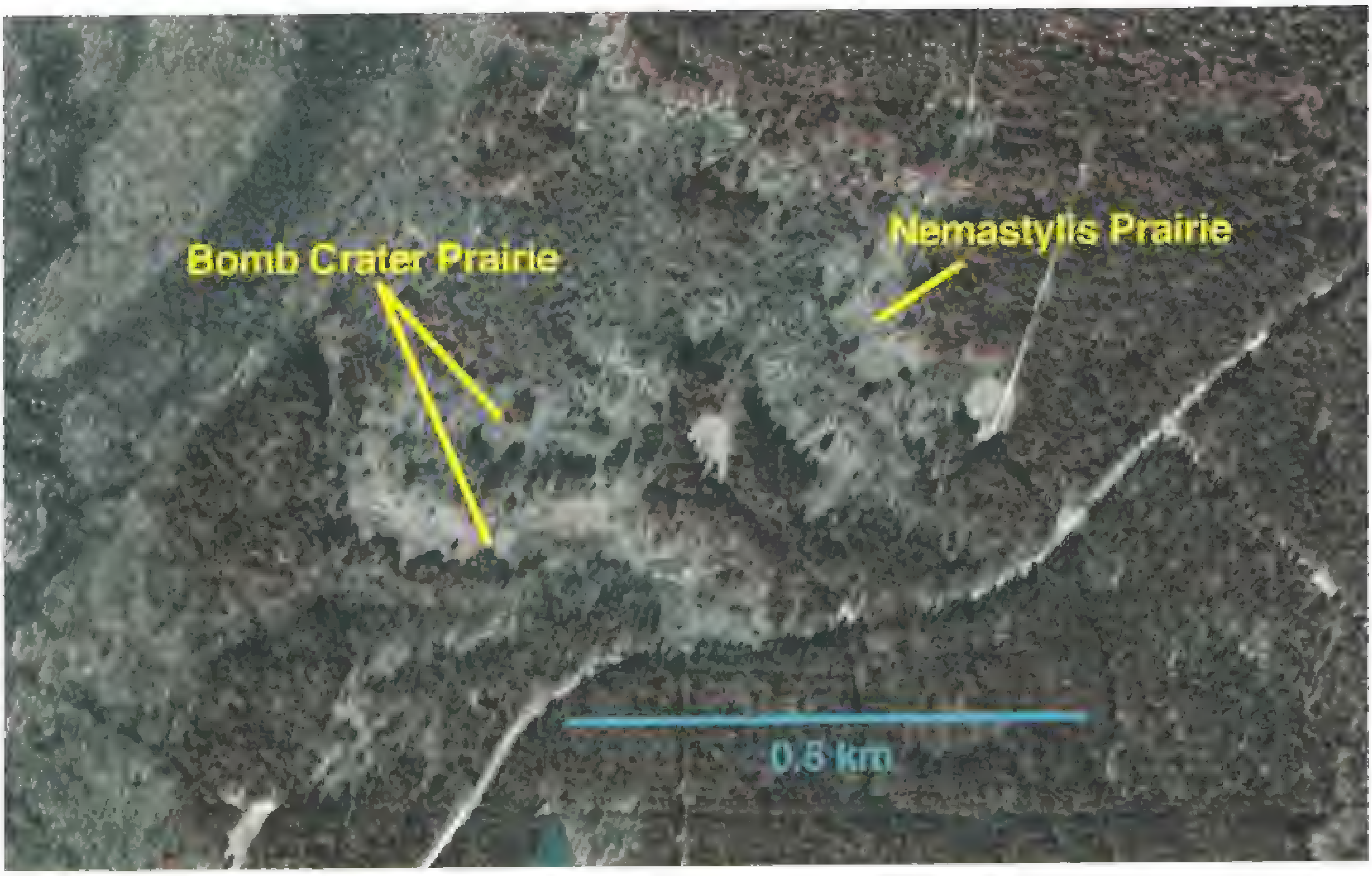

Fig. 2. Aerial photograph of Morse Clay Prairie.

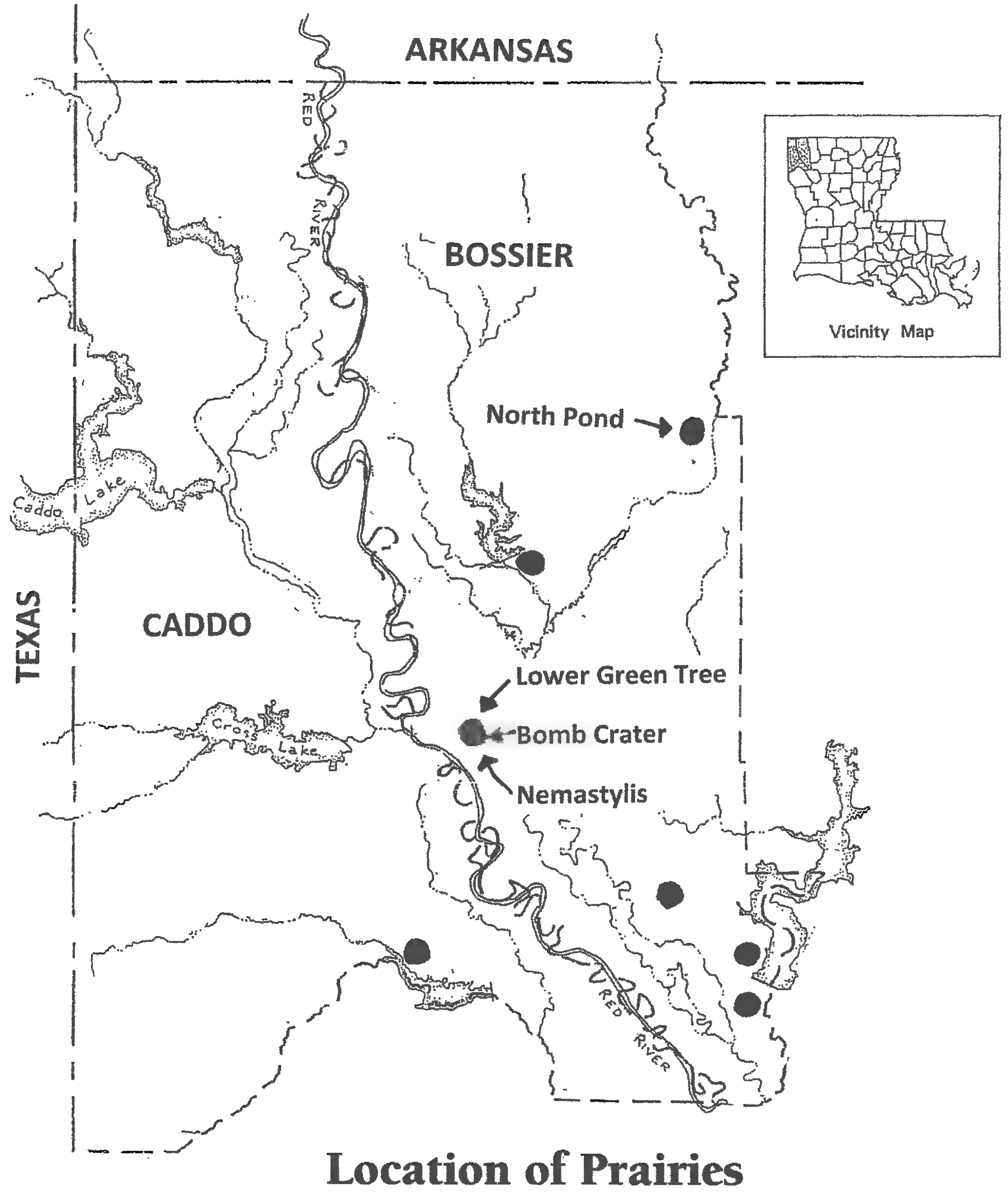

Fig. 3. Location of Morse Clay prairies in Caddo and Bossier parishes, Louisiana. Unlabeled dots are locations of other Morse Clay prairies that were briefly surveyed. Labeled dots are the location of the prairies that were intensively studied.

While it is clear that the best remnants of this prairie type occur on Barksdale AFB and Bodcau WMA (McInnis 1997), these sites can scarcely be described as "relatively undisturbed." Thus, our best estimate becomes largely subjective based on our experience with other prairies in the West Gulf Coastal Plain (including other Morse Clay prairies surveyed as part of this study but not reported here [MacRoberts & MacRoberts 2007b]). Assessing such characteristics as native biotic diversity and presence/absence of exotics (McInnis 1997), we determined that the four Morse Clay prairies we studied had 10 (6%) exotics, which indicates

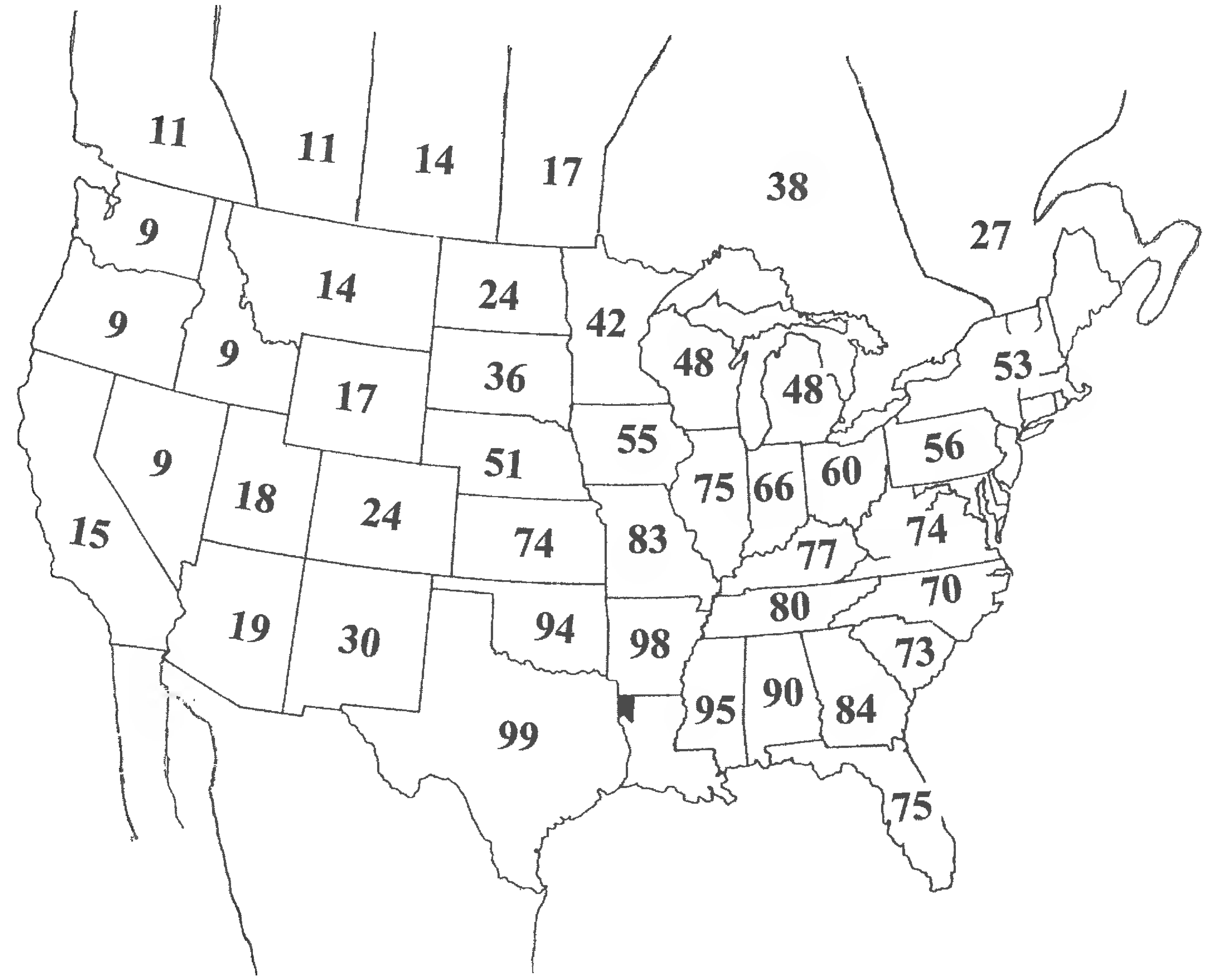

Fig. 4. North American distribution of native Morse Clay prairie species. Numbers are percent of total that occur in state, province, or region. Bossier and Caddo parishes, the location of Morse Clay prairies, are shown in northwestern Louisiana.

little disturbance (MacRoberts et al. 2008). The Barksdale AFB and Bodcau WMA prairies are therefore important because they present a standard by which the quality of other Morse Clay prairies may be evaluated, but care should be exercised in making general conclusions from these few scattered remnants, all of which have undergone a long history of anthropogenic disturbance.

The North American geographic distribution of Morse Clay Prairie species is decidedly eastern. However, a comparison of their distribution with that of Caddo Parish flora as a whole (MacRoberts & MacRoberts 2007a) shows that their affinities are slightly more central and western than are those of Caddo Parish (Caddo Parish is just west of Bossier Parish and also has Morse Clay prairies, see Fig. 3). This might be expected since there are many habitats in Caddo Parish that are exclusively eastern (e.g., swamps); whereas prairies generally have a central and western component.

ACKNOWLEDGMENTS

This work was partly supported by contract 64332 from the Louisiana Department of Wildlife and Fisheries. Bruce Holland, Natural Resources Manager, Barksdale AFB, facilitated access to the study sites. We also thank Suzanne Odom, Forester, U.S. Army Corps of Engineers, for permission to work on Bodcau WMA and informing us about the management history of Bodcau. We thank Richard McMullen, formerly of Louisiana Department of Wildlife and Fisheries, for taking us out several times on Bodcau WMA to show

Table 1. Vascular flora of four Morse clay prairies (**NP** = North Pond Prairie, **LGT** = Lower Green Tree Prairie, **BC** = Bomb Crater Prairie, and **N** = Nemastylis Prairie. * = exotic species).

Acanthaceae
Ruellia humilis Nutt., NP, LGT, BC, N, MM 7780, 7698, 7515, 7484
Agavaceae
Manfreda virginica (L.) Rose, NP, LGT, N, MM 7477
Yucca louisianensis Trel., LGT, MM 7857
Anacardiaceae
Toxicodendron radicans (L.) Kuntze, NP, LGT, BC (no specimen collected)
Apiaceae
Eryngium yuccifolium Michx., BC, N, MM 7540
Trepocarpus aethusae Nutt. ex DC., NP, LGT, MM 7781
Aquifoliaceae
Ilex decidua Walt., NP, LGT, BC, MM 7512
Araceae
Sabal minor (Jacq.) Pers., NP, MM 7504
Asclepiadaceae
Asclepias verticillata L., NP, LGT, BC, N, MM 7786, 7560, 7961
Asclepias viridis Walt., NP, MM 7689, 7562
Asteraceae
Ambrosia artemisiifolia L., LGT, N (no specimen collected)
Ambrosia bidentata Michx., NP, MM 7523
Ambrosia psilostachya DC., NP, MM 7522
Ambrosia trifida L., LGT, MM 7556
Arnoglossum plantagineum Raf., NP, LGT, BC, N, MM 7690, 7713
Baccharis halimifolia L., NP, LGT, BC, N, MM 7509, 7531
Boltonia diffusa Ell., N, MM 7965
Cirsium horridulum Michx., NP, LGT, BC, MM 7685, 7712
Coreopsis lanceolata L., NP, LGT, BC, N, MM 7783, 7688, 7718
Coreposis palmata Nutt., BC, MM 7793, 7845
Echinacea pallida (Nutt.) Nutt., NP, LGT, MM 7691
Echinacea sanguinea Nutt., BC, MM 7791, 7789
Erigeron strigosus Muhl. ex Willd., NP, LGT, BC, N, MM 7703, 7707, 7479, 7716
Erigeron tenuis Torr. & A. Gray, N, MM 7630
Eupatorium serotinum Michx., BC, N, MM 7536
Eurybia hemispherica Alexander) Nesom, BC, N, MM 7530
Gaillardia aestivalis (Walter) H. Rock, LGT, MM 7480
Helianthus hirsutus Raf., LGT, BC, N, MM 7794, 7846, 7858
Heterotheca subaxillaris (Lam.) Britt. & Rusby, LGT, MM 7558
Iva annua L., NP, LGT, BC, N, 7557, 7840
Liatris aspera Michx., NP, LGT, BC, N, MM 7500, 7553, 7485, 8054
Liatris squarrosa (L.) Michx., BC, MM 7454
Marshallia caespitosa Nutt. ex DC., LGT, N, MM 7715
Parthenium integrifolium L., NP, LGT, BC, N, MM 7460, 7853
Rudbeckia hirta L., LGT, N, MM 7859
Silphium integrifolium Michx., NP, MM 7517
Silphium laciniatum L., BC, MM 7459, 7847
Solidago canadensis L., LGT, MM 7552
Solidago nitida Torr. & A. Gray, NP, BC, N, MM 7498
Solidago rigida L., LGT, BC, N, MM 7557, 7849, 7841
Symphyotrichum drummondii (Lindl.) Nesom, LGT, MM 7472
Symphyotrichum laevis (L.) A. & D. Löve, LGT, BC, N, MM 7478, 7572, 7838, 8057, 8115
Symphyotrichum lateriflorum (L.) Löve & Löve, NP, LGT, MM 7579
Symphyotrichum ontarione (Weigand) Nesom, LGT, MM 7575, 7576
Symphyotrichum oolentangiensis (Riddell) Nesom, LGT, BC, N, MM 7573, 7966
Symphyotrichum patens (Ait.) Nesom, NP, LGT, BC, N, MM 7499, 7482, 7546, 8116
Symphyotrichum pilosum (Willd.) Nesom, NP, LGT, BC, N, MM 7554
Symphyotrichum praealtum (Poir.) Nesom, NP, N, MM 7570
Symphyotrichum pratense (Raf.) Nesom, BC, N, 7962, 8114
Vernonia texana (A. Gray) Small, NP, LGT, MM 7492
Bignoniaceae
Campsis radicans (L.) Seem. ex Bureau, LGT, N, MM 7837
Boraginaceae
Onosmodium bejariense DC. ex A. DC., NP, MM 7519
Campanulaceae
Lobelia appendiculata A.DC., NP (no specimen collected)
Caprifoliaceae
**Lonicera japonica* Thumb., BC, MM 7535
Symphoricarpus orbiculatus Moench., BC, MM 7527
Viburnum rufidulum Raf., NP, BC, MM 7508
Convolvulaceae
Dichondra carolensis Michx., LGT, MM 7722
Cornaceae
Cornus drummondii C.A. Mey., BC, MM 7532
Cupressaceae
Juniperus virginiana L., LGT, MM 7580
Cuscutaceae
Cuscuta pentagona Engelm., N, MM 7839, 8110
Cyperaceae
Carex abscondita Mack., NP, MM 7702
Carex cherokeensis Schwein., NP, LGT, BC, N, MM 7636, 7624
Carex meadii Dewey, NP, LGT, N, MM 7632, 7622, 8136
Fimbristylis puberula (Michx.) Vahl, BC, MM 7708
Scleria ciliata Michx., NP, MM 7779b
Scleria oligantha Michx., NP, MM 7779a
Ebenaceae
Diospyros virginiana L., NP, LGT, BC, N, MM 7503, 7534
Euphorbiaceae
Chamaesyce nutans (Lag.) Small, LGT, MM 7559b, 7582
Croton monanthogynus Michx., NP, LGT, N, MM 7520, 7469, 7964
Euphorbia corollata L., LGT (no specimen collected)
Tragia urticifolia Michx., NP, LGT, BC, N, MM 7488, 7709
Fabaceae
Acacia angustissima (Mill.) Kuntze, NP, LGT, BC, N, MM 7470
Astragalus distortus Torr. & A. Gray, NP, LGT, N, MM 7628, 7571, 7625, 7471
Baptisia bracteata Muhl. ex Elliott, NP, LGT, BC, N, MM 7629, 7618

Centrosema virginianum (L.) Benth., LGT, MM 7854
Cercis canadensis L., BC, MM 7526
Chamaecrista fasciculata (Michx.) Greene, NP, MM 7494
Dalea candida Willd., NP, BC, N, MM 7777, 7792
Dalea purpurea Vent., NP, LGT, BC, N, MM 7456
Desmanthes illinoensis (Michx.) MacM. ex B.L. Robins & Fern., LGT, BC, N, MM 7855
Galactia volubilis (L.) Britt., NP, LGT, BC, N, MM 7851
Gleditsia triacanthos L., NP (no specimen collected)
**Lespedeza cuneata* (Dum. Cours.) G. Don, NP, BC, MM 7493
**Medicago lupulina* L., NP, MM 7785
Mimosa nuttallii (DC.) B.L. Turner, N, MM 8183
Mimosa strigillosa Torr. & A. Gray, NP, LGT, BC, N, MM 7496
Neptunia lutea (Leavenw.) Benth., NP, LGT, BC, N, MM 7516, 7481
**Trifolium dubium* Sibth., NP, MM 7693

Fagaceae
Quercus stellata Wangenh., NP, BC, MM 7843

Gentianaceae
**Centaurium pulchellum* (Sw.) Druce, LGT, MM 7852
Sabatia campestris Nutt., NP, N, MM 7782

Iridaceae
Nemastylis geminiflora Nutt., LGT, N, MM 7619
Sisyrinchium albidum Raf., LGT, BC, MM 7620
Sisyrinchium langloisii Greene, NP, MM 7695, 7633

Lamiaceae
**Prunella vulgaris* L., NP, LGT, BC, N, MM 7687, 7717
Pycnanthemum tenuifolium Schrad., BC, MM 7529
Salvia azurea Michx. ex Lam., LGT, BC, N, MM 7550, 7863, 8113
Salvia lyrata L., NP, LGT, BC, N, MM 7635, 7623

Liliaceae
Allium canadense L., NP, BC, N, MM 7699, 7706
Nothoscordum bivalve (L.) Britt., NP, LGT, MM 7637, 7626

Lythraceae
Lythrum alatum Pursh, BC, LGT, NP, N, MM 7856

Moraceae
Maclura pomifera (Raf.) Schenid., NP, MM 7501

Oleaceae
Fraxinus pennsylvanica Marsh, NP, LGT, BC, N, MM 7510, 7533

Onagraceae
Oenothera speciosa Nutt., NP, N, MM 7701

Orchidaceae
Spiranthes laciniata (Small) Ames, NP, MM 7788

Oxalidaceae
Oxalis corniculata L., NP, MM 7638, 7700

Pinaceae
Pinus echinata Mill., NP, MM 7514

Poaceae
Andropogon gerardii Vitman, NP, LGT, BC, N, MM 7545, 7537, 7466
Andropogon glomeratus (Walt.) B.S.P., NP, LGT, BC, N, MM 7538
Andropogon virginicus L., NP, LGT, MM 7567
Aristida oligantha Michx., NP, MM 7568
**Botriochloa ischaemum* L., NP, MM 7583
Bothriochloa longipaniculata (Gould) Allred & Gould, LGT, MM 7861, 7487
Dichanthelium aciculare (Desv. ex Poir.) Gould & Clark, LGT, BC, NP, N, MM 7719, 7710, 7694
Elymus virginicus L., NP, LGT, BC, MM 7506, 7473
Eragrostis lugens Nees, N, MM 8056, 8112, 7963
Eragrostis spectabilis (Pursh) Steud., NP, LGT, N, MM 7542
Panicum anceps Michx., NP, BC, MM 7864
Paspalum floridanum Michx., NP, LGT, N, MM 7544
**Paspalum dilatatum* Poir., LGT, MM 7581, 7586
Paspalum laeve Michx., NP, MM 7867
Schizachyrium scoparium (Michx.) Nash, NP, LGT, BC, N, MM 7564, 7541
Setaria parviflora (Poir.) Kerguelen, LGT, BC, N, MM 7474, 7548
**Setaria pumila* (Poir.) Roem. & Schult., NP, MM 7565
Sorghastrum nutans (L.) Nash, LGT, BC, N, MM 7539, 8117, 8055
Sphenopholis obtusata (Michx.) Scribn., NP, LGT, BC, N, MM 7714, 7711
Sporobolus asper (Beauv.) Kunth, NP (no specimen collected)
Sporobolus compositus (Poir.) Merr., NP, LGT, MM 7566, 7574, 7543
Tridens strictus (Nutt.) Nash, NP, MM 7569
Tripsicum dactyloides (L.) L., NP, MM 7865

Polemoniaceae
Phlox pilosa L., NP, MM 7696

Ranunculaceae
Amenone berlandieri Pritz., NP, MM 7631
Delphinium carolinianum Walt., NP, MM 7784

Rhamnaceae
Berchemia scandens (Hill) K. Koch, NP, LGT, BC, N, MM 7513

Rosaceae
Crataegus brachyacantha Sarg. & Engelm., NP, MM 7502, 7495
Crataegus marshallii Egglest., NP (no specimen collected)
Crataegus spathulata Michx., NP, MM 7505
Rosa carolina L., NP, MM 7490, 7778
Rosa setigera Michx., BC, N, MM 7790, 7850
Rubus trivialis Michx., NP, LGT, N, MM 7634

Rubiaceae
Hedyotis nigricans (Lam.) Fosberg, LGT, BC, N, MM 7547, 7476
Houstonia micrantha (Skinner) Terrell, NP (no specimen collected)
Houstonia purpurea L. var. *calycosa* A. Gray, NP, MM 7497, 7697

Sapotaceae
Sideroxylon lanuginosum Michx., NP, LGT, BC, N, MM 7511, 7483

Scrophulariaceae
Agalinis heterophylla (Nutt.) Small, NP, LGT, MM 7525, 7555
Agalinis tenuifolia (Vahl) Shinners, NP, N, MM 7563, 8111
Aureolaria grandiflora (Benth.) Pennell, BC, MM 7467
Pedicularis canadensis L., BC (no specimens collected)
Penstemon laxiflorus Pennell, NP, BC, N, (no specimens collected)
Penstemon tubaeflorus Nutt., N, MM 8182, 7686, 7705

Smilaceae
Smilax bona-nox L., NP, LGT, BC, N, MM 7518, 7475
Ulmaceae
Ulmus alata Michx., NP, LGT, MM 7507
Ulmus crassifolia Nutt., LGT, BC, N, MM 7528
Valerianaceae
Valerianella radiata (L.) Dufr., NP, MM 7692
Verbenaceae
Glandularia canadensis (L.) Nutt., NP, LGT, BC, N, MM 7627, 7621
Lippia nodiflora (L.) Michx., NP, MM 7787, 7491
**Verbena brasiliensis* Velloso, NP, MM 7521
Verbena halei Small, NP, N, MM 7866
Vitaceae
Ampelopsis arborea (L.) Koehne, LGT, BC, N, MM 7860

Table 2. Species richness in Morse Clay Prairies.

Plot and plot size (ha)	No. of	Average species (range)
North Pond Prairie		
0.0001	2	21(20–22)
0.001	2	30.5(28–33)
0.1	1	105
Lower Green Tree Prairie		
0.0001	2	22(21–23)
0.001	2	28.5(28–29)
0.1	1	85
Bomb Crater Prairie		
0.0001	2	11.5(5–18)
0.001	2	18(17–19)
0.1	1	75
Nemastylis Prairie		
0.0001	2	23.5(21–26)
0.001	2	30.5(25–36)
0.1	1	76
Total		
0.0001	8	19.5(5–26)
0.001	8	26.9(17–36)
0.1	4	85.3(75–105)

Table 3. Index of Similarity (Sorenson's) among four Morse Clay prairies (**NP** = North Pond Prairie, **LGT** = Lower Green Tree Prairie, **BC** = Bomb Crater Prairie, and **N** = Nemastylis Prairie). Formula is $(2C/(A+B)) \times 100$ where C = number of species in common between two samples, A = total species in sample A, and B = total species in sample B.

	NP	LGT	BC
NP	-	-	-
LGT	56	-	-
BC	49	61	-
N	53	66	72

Table 4. Soils data for Morse Clay Prairies in northwest Louisiana.

Sample	pH	Calcium (ppm)	Copper (ppm)	Magnesium (ppm)	Phosphorous (ppm)	Potassium (ppm)	Sodium (ppm)	Sulfur (ppm)	Zinc (ppm)	Soil Texture
LGT-Woods above prairie	4.8	417.3	1.4	408.2	7.7	101.4	26.4	7.6	1.4	Silt loam
LGT- Upper part of prairie	8.1	6352.8	1.7	763.8	4.2	272.6	13.6	8.2	1.1	Silty clay
LGT- Lower part of prairie	8.2	6682.5	7.7	742.9	3.7	314.1	7.7	7.9	22.2	Silty clay loam
LGT-Woods below prairie	5.2	1685.6	1.1	832.1	7.4	187.1	10.2	12.8	1.4	Silty clay loam
BC-Woods above prairie	4.6	163.1	0.6	143.4	3.1	46.7	7.2	8.7	0.6	Silt loam
BC-Upper part of prairie	7.2	4363.1	4.7	857.0	6.2	269.9	12.4	7.5	1.6	Silty clay
BC-Lower part of prairie	8.1	7854.0	1.9	1010.1	4.0	365.3	6.4	10.3	1.7	Silty clay
BC-Woods below prairie	7.2	4674.7	1.6	1097.9	4.1	365.8	11.8	9.4	0.9	Silty clay
NP-Woods above prairie	4.8	540.1	0.5	539.0	7.7	103.6	16.6	6.3	3.3	Silty clay loam
NP-Upper part of prairie	6.8	2917.8	1.7	1301.0	3.4	293.4	11.7	7.4	0.8	Silty clay loam
NP- Lower part of prairie	8.3	8514.4	1.6	959.8	2.4	340.2	8.2	9.3	0.6	Silty clay loam
N – Woods above prairie	5.6	344.5	0.2	74.0	5.9	33.3	9.9	10.7	0.5	Very fine sandy loam
N – In center of prairie	7.3	5830.2	1.8	734.9	8.6	321.4	418.3	69.6	2.5	Silty clay loam
N – Woods below prairie	7.4	6118.1	2.8	590.9	11.3	332.5	14.3	20.4	2.7	Silty clay loam

us prairies and share with us his knowledge of the plant life of the area. John Haygood, formerly a Louisiana Department of Wildlife and Fisheries biologist, provided information on the condition of Bodcau prairies in the 1950s. Bob O'Kennon, Botanical Research Institute of Texas, Guy Nesom, and Charles Allen aided with plant identification. Theo Witsell, Arkansas Natural Heritage Commission, provided information on the Arkansas Morse Clay prairies. Latimore Smith, Dennis Bell, and an anonymous reviewer made useful suggestions that improved the manuscript.

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FLORISTICS OF UPLAND SHORTLEAF PINE/OAK-HICKORY FOREST IN NORTHWESTERN LOUISIANA

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ABSTRACT

The structure of upland shortleaf pine forest and upland shortleaf pine/oak-hickory forest that occurred historically in the Upper West Gulf Coastal Plain is poorly understood. This is primarily because most of it was destroyed before botanists and ecologists were able to describe it. What little is known centers mainly on trees and is derived largely from historical information. The herbaceous layer is even more poorly understood. We describe the herbaceous layer of a shortleaf pine/oak-hickory forest in northwestern Louisiana. The study site is not pristine, but its herbaceous layer may represent what naturally accompanied this type of forest in pre-settlement times.

RESUMEN

La estructura del bosque de pino de hoja corta y bosque de pino de hoja corta /roble-nogal americano que existió históricamente en la zona alta de la llanura costera del West Gulf está poco entendido. Esto se debe en primer lugar a que la mayoría fue destruido antes que los botánicos y ecólogos pudiesen describirlo. Lo poco que se sabe se centra principalmente en los árboles y se deriva mayormente de información histórica. El estrato herbáceo está aún menos conocido. Se describe el estrato herbáceo del bosque de pino de hoja corta / roble-nogal americano en el noroeste de Louisiana. El lugar de estudio no es prístino, pero su estrato herbáceo puede representar lo que de modo natural acompañaba a este tipo de bosque en los tiempos previos a los asentamientos.

INTRODUCTION

Virtually no upland shortleaf pine/oak-hickory forest survived late nineteenth and early twentieth century logging and little is known about this ecosystem, which apparently was once common in the Upper West Gulf Coastal Plain (southern Arkansas, southeastern Oklahoma, northern Louisiana, and northeastern Texas) (Williams & Smith 1995; Carr 2000; Bragg 2002, 2003, 2008; Diggs et al. 2006; MacRoberts & MacRoberts 2008a, 2008b; Masters 2008 and references therein). Historical accounts and photographs indicate that shortleaf pine often dominated and was sometimes found in pure or near pure stands on drier and fire-prone upland sites, but that more often it occurred in association with oak and hickory (Bragg 2002, 2008; Lester et al. 2005). Many stands appeared to be open—"park like"—with a rich "high-light" community of herbaceous plants (Bragg 2002), but like most forest descriptions of the nineteenth and twentieth centuries, the herbaceous layer was ignored and certainly never described in detail (Gilliam 2007). Consequently, not only is little known about the over-story of these forests but even less is known about the herbaceous layer (Carr 2000; Bragg 2002, 2008). The destruction of the shortleaf pine/oak-hickory forest community was so complete, not only through logging but fire suppression and agriculture, that an understanding of this community depends almost entirely on historical documents, notably land survey records and forester's descriptions that emphasize trees (but not always species of trees)(Bragg 2002, 2003, 2004, 2008; MacRoberts & MacRoberts 2005; Nowacki & Abrams 2008; see also Diggs et al. 2006; Van Kley 2006).

In the course of our work on another project on Barksdale Air Force Base, Bossier Parish, in northwestern Louisiana, we found several areas where shortleaf pine was the dominant canopy species, where fire had been used as a management tool, and where the herbaceous layer appeared to be intact.

We took the opportunity to study the flora of one of these sites, recognizing that it was not pristine but that perhaps it was as close to "natural" as now exists. Our main interest was the herbaceous layer. In the few places where shortleaf pine/oak-hickory forest exists, the understory has been radically altered by

fire suppression: fire intolerant and shade-adapted species have replaced the naturally occurring pyrogenic heliophytes (Bragg 2002; Gilliam 2007; Nowacki & Abrams 2008).

STUDY SITE

The study area is located on Barksdale Air Force Base, Bossier Parish, Louisiana, (T17NR12WS2). Natural Areas on Barksdale AFB have been described by McInnis (1997). Land plat records from the 1830s show that the study area was, in general, a pine-oak-hickory forest (McInnis 1997; Lester et al. 2005). While the area has been repeatedly logged, it is still oak-pine-hickory today but is predominantly shortleaf pine. Canopy trees on the study plots today are only shortleaf pine (Fig. 1). In the mid 1990s, the area's pine was thinned from approximately a basal area of 70 to about 45. Removal of pine increased hardwood growth, which was subsequently removed by helicopter application of the herbicide Arsenal. The area is currently controlled burned on a two-to-three year rotation with prescribed fire in the early months (generally January–February) of the year. The area was last burned in February 2008. Soils are the Sacul series, typically moderately well-drained, acid fine sandy loam, thermic Aquic Hapludults, with a clay underlayer along the ridgetops in the uplands (Kilpatrick et al. 1990).

METHODS

To obtain a species list and to determine species richness, we established two 0.1 ha plots, each with two nested 0.001 ha plots and two nested 0.0001 ha plots about 100 m apart on ridge tops (Fig. 1). All species in the plots were recorded and most species in the plots were collected. Voucher specimens are deposited at the Louisiana State University in Shreveport Herbarium LSUS). We visited the site monthly between 2 April 2008 and 21 October 2008.

To determine the geographical distribution of species in the sample, we established a grid of 114 km to a side across the West Gulf Coastal Plain and, using Turner et al. (2003), Thomas and Allen (1993–1998), and USDA NRCS (2008), plotted the distribution of species in the Barksdale AFB shortleaf pine/oak-hickory forest study plots.

Soil samples were collected from the upper 30 cm in the center of each 0.1 ha plot. These were analyzed by the Soil Testing and Plant Analysis Laboratory, Louisiana State University, Baton Rouge.

RESULTS

The flora of the 0.2 ha study area (two 0.1 ha plots) is given in Table 1. Table 2 summarizes the species richness data from the plots. Table 3 gives the soil sample results. Figure 2 gives the results of the geographical distribution analysis.

The two 0.1 ha plots contained 122 species. Taxa from the Asteraceae, Fabaceae, and Poaceae dominated and accounted for 46 percent of the flora. The mean number of species in the two 0.1 ha plots was 99.5 species (92 and 107), the mean number in the four 0.001ha plots was 30.25 species (range 28 to 33) and the mean number in the four 0.0001 ha plots was 17.5 species (range 15 to 19). The soils have low pH (5.2 and 5.4 in two samples) and are generally low in nutrients (see Table 3). The data in Figure 2 indicate that the species found in the study plots are not specific to any particular region of the West Gulf Coastal Plain but occur throughout the area.

DISCUSSION

The Barksdale AFB shortleaf pine/oak-hickory forest flora is remarkably similar to upland longleaf pine forest/savanna in central Louisiana and southeastern Texas (see Harcombe et al. 1993; Van Kley 1999a, 1999b and especially Carr 2000 and references therein). Turner et al. (1999) listed the species groups identified during multivariate analysis to be important in distinguishing among communities in the longleaf pine ecoregion of Texas and Louisiana. These species are abundant enough to occur consistently within a community, but are specialized enough to be present in some communities but absent or markedly less abundant in others. We

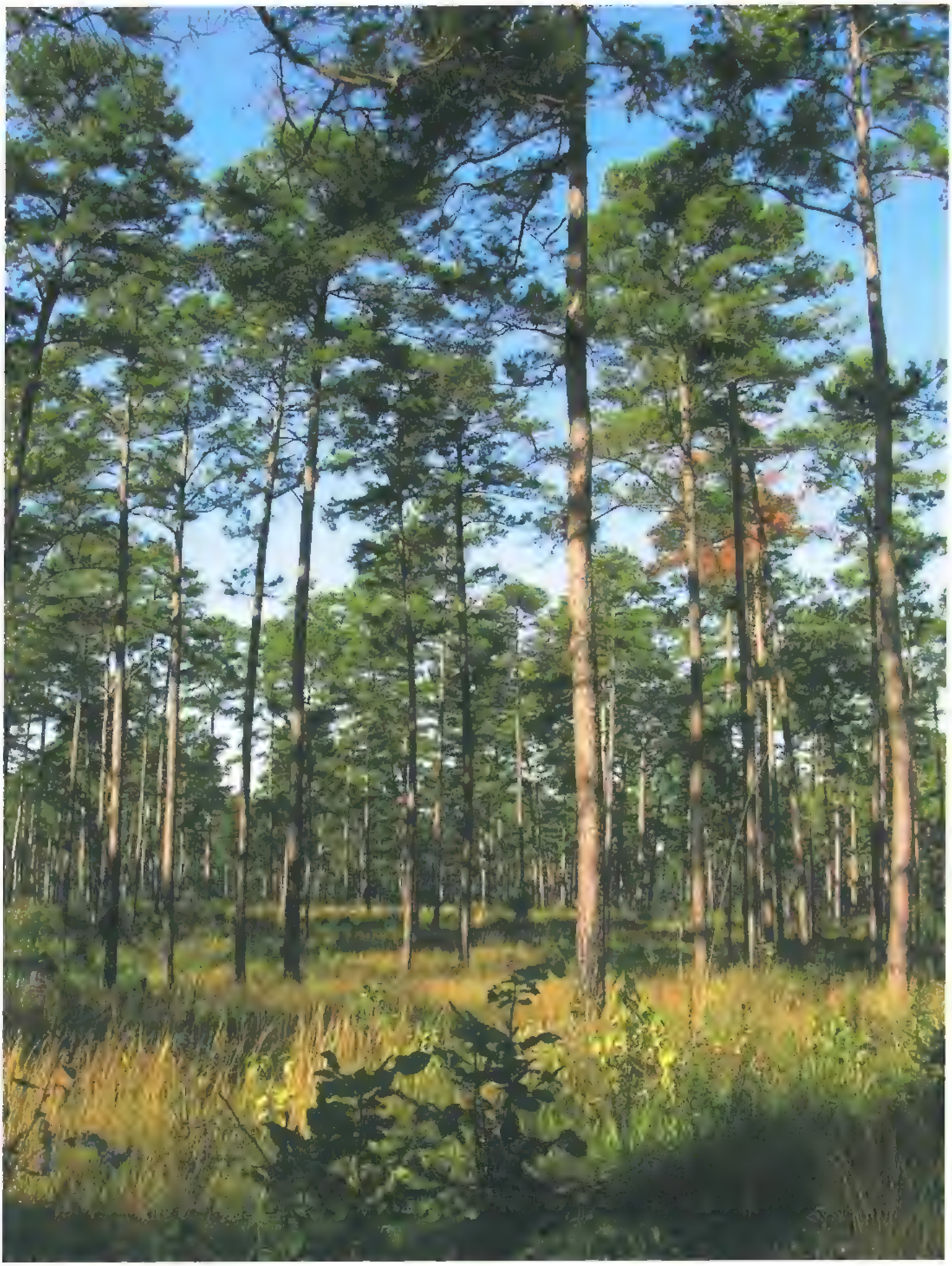

Fig. 1. Barksdale Air Force Base shortleaf pine/oak-hickory forest study site.

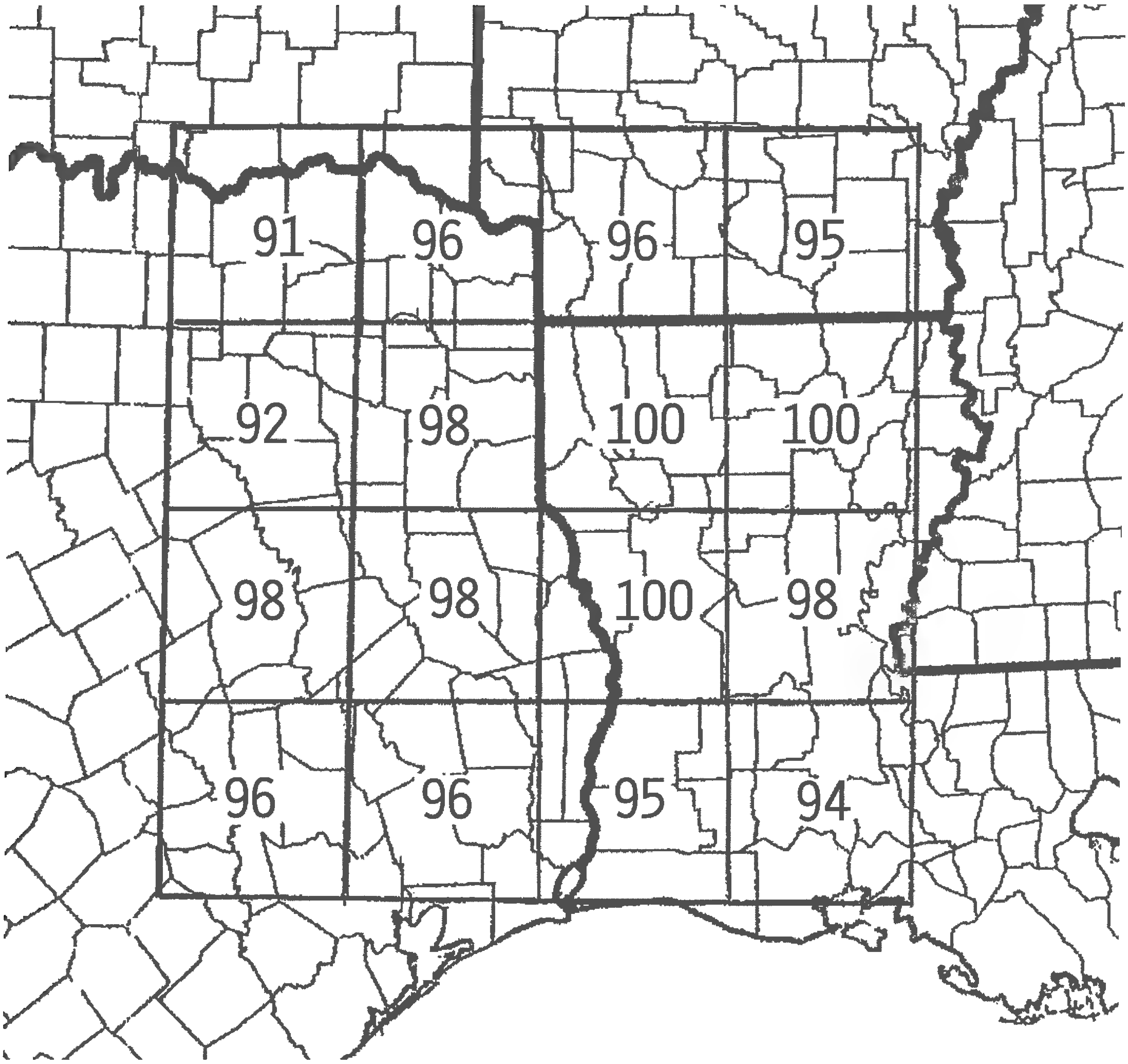

Fig. 2. Percentage of Barksdale AFB shortleaf pine/oak-hickory forest study plot species occurring across the West Gulf Coastal Plain. The grids are 114 km on a side.

found that our shortleaf pine/oak-hickory forest plots had 71 percent of the species in their "Schizachyrium group," which characterizes the upland longleaf pine forest/savanna. This similarity between Barksdale AFB shortleaf pine/oak-hickory forest and particularly upland longleaf pine forest/savanna is reinforced by the plants listed by the Louisiana Natural Heritage Program (2008) as typifying western upland longleaf pine forest: 63 percent occurred in the Barksdale AFB plots. Turning to more detailed studies, 53 percent of the Barksdale AFB shortleaf pine/oak-hickory forest species occur in four 0.1 ha upland longleaf pine forest/savanna plots in central Louisiana on the Kisatchie National Forest (MacRoberts et al. 2002), and 60 percent of the Barksdale AFB shortleaf pine/oak-hickory forest species occurred in eight 0.1 ha upland longleaf pine savanna/forest plots in eastern Texas on the Sabine National Forest (Philipps et al. 2007). An Index of Similarity (Sørensen) between the Barksdale shortleaf pine/oak-hickory forest flora and the flora of upland longleaf pine forest/savanna in both the Kisatchie National Forest in central Louisiana and the Sabine National Forest in eastern Texas (MacRoberts et al. 2002; Philipps et al. 2007) gives figures of 46.4 and 46.5, respectively. Considering the differences in sample size (Barksdale AFB sample, 122 species; Kisatchie

Table 1. Species in the two 0.1 ha study plots. Numbers refer to MacRoberts and MacRoberts collections. The lack of a number indicates that a specimen was not collected.

Acanthaceae
Ruellia pedunculata Torr. & A. Gray, 8186
Aceraceae
Acer rubrum L., 8284
Anacardiaceae
Rhus copallinum L., 8316
Toxicodendron radicans (L.) Kuntze
Aristolochiaceae
Aristolochia reticulata Jacq.
Asclepiadaceae
Asclepias variegata L., 8185
Asteraceae
Ambrosia artemisiifolia L., 8295, 8354
Antennaria parlinii Fern., 8146, 8221
Baccharis halimifolia L., 8265
Conyza canadensis (L.) Cronquist, 8340
Coreopsis lanceolata L., 8195
Erigeron strigosus Muhl. ex Willd., 8187
Eupatorium perfoliatum L., 8374
Eupatorium rotundifolium L., 8286
Eurybia hemispherica (Alexander) Nesom, 8338, 8359
Euthamia leptocephala (T. & G.) Greene 8336
Gamochaeta purpurea (L.) Cabrera, 8208, 8222
Helianthus hirsutus Raf., 8262, 8277
Hieracium gronovii L., 8288
Lactuca canadensis L.
Liatris pycnostachya Michx.
Liatris squarrosa (L.) Michx., 8287
Liatris squarrulosa Michx., 8318, 8352
Pityopsis graminifolia (Michx.) Nutt., 8278, 8347
Pseudognaphalium obtusifolium (L.) Hilliard & Burt, 8349
Rudbeckia hirta L., 8270
Solidago altissima L., 8377
Solidago odora Aiton, 8291
Solidago petiolaris Aiton, 8356, 8376
Solidago radula L., 8317, 8357
Solidago rigida L.
Symphytorichum dumosum (L.) Nesom
Symphyotrichum lateriflorum (L.) Á. Löve & D. Löve, 8380
Symphyotrichum patens (Aiton) Nesom, 8209
Verbesina helianthoides Michx., 8194
Vernonia texana (A. Gray) Small, 8271
Campanulaceae
Lobelia appendiculata A. DC., 8193
Triodanis perfoliata (L.) Nieuwl.
Cistaceae
Lechea tenuifolia Michx., 8290
Clusiaceae
Hypericum drummondii (Grev. & Hook.) T. & G., 8355
Hypericum hypericoides (L.) Crantz
Commelinaceae
Commelina erecta L.
Tradescantia hirsutiflora Bush, 8142, 8190
Cyperaceae
Carex complanata Torr. & Hook., 8207, 8211
Cyperus echinatus (L.) Wood, 8202, 8213, 8272
Rhynchospora harveyi W. Boott., 8274
Scleria oligantha Michx., 8203
Dennstedtiaceae
Pteridium aquilinum (L.) Kuhn, 8141
Dioscoreaceae
Dioscorea villosa L., 8137
Ebenaceae
Diospyros virginiana L., 8305, 8298
Ericaceae
Vaccinium arboreum Marshall, 8276
Euphorbiaceae
Acalypha monococca (Engelm. ex A. Gray) L. Mill. & Gandhi, 8282, 8293
Chamaesyce nutans (Laq.) Small, 8341
Euphorbia corollata L., 8145, 8189
Fabaceae
Baptisia nuttalliana Small, 8197
Centrosema virginianum (L.) Benth., 8260, 8321
Crotalaria sagittalis L., 8301
Desmodium ciliare (Muhl. ex Willd.) D.C., 8263, 8280
Lespedeza hirta (L.) Hornem.
Mimosa nuttallii (DC.) B.L. Turner, 8269
Stylosanthes biflora (L.) Britton, Sterns, & Poggenb., 8198
Tephrosia virginiana (L.) Pers., 8279
Vicia caroliniana Walt., 8149
Fagaceae
Quercus falcata Michx., 8373
Quercus marilandica Münchh.
Quercus phellos L., 8292
Quercus stellata Wang., 8372
Hamamelidaceae
Liquidambar styraciflua L., 8266
Iridaceae
Sisyrinchium albidum Raf., 8140
Juglandaceae
Carya sp., 8256
Juncaceae
Juncus dudleyi Wiegand, 8212
Luzula bulbosa (A.W. Wood) Smyth, 8147
Lamiaceae
Monarda fistulosa L., 8267
Salvia azurea Lam., 8356
Salvia lyrata L., 8139
Lauraceae
Sassafras albidum (Nutt.) Nees
Liliaceae
Allium canadense L., 8188
Loganiaceae
Gelsemium sempervirens (L.) St. Hil., 8304
Oleaceae
Chionanthus virginica L., 8296
Oxalidaceae
Oxalis dillenii Jacq., 8191
Oxalis violacea L., 8144, 8210
Pinaceae
Pinus echinata P. Mill., 8281

Table 1. (continued)

Plantaginaceae
Plantago virginica L., 8200
Poaceae
Agrostis hyemalis (Walt.) Britton, Sterns, & Poggenb., 8201, 8218
Andropogon gerardii Vitman, 8315
Andropogon ternarius Michx.
Aristida purpurascens Poir., 8350, 8351, 8375
Chasmanthium sessiliflorum (Poir.) Yates, 8283
Dichanthelium aciculare (Desv. ex Poir.) Gould & Clark, 8217
Dichanthelium dichotomum (L.) Gould, 8204, 8215, 8216
Dichanthelium ravenelii (Scribn. & Merr.) Gould, 8206
Dichanthelium scoparium (Lam.) Gould, 8259
Dichanthelium sphaerocarpon (Elliott) Gould, 8214
Eragrostis spectabilis (Pursh) Steud., 8342, 8344, 8379
Panicum anceps Michx., 8273, 8302
Paspalum setaceum Michx., 8258, 8348
Schizachyrium scoparium (Michx.) Nash
Sphenopholis obtusata (Michx.) Scribn., 8205, 8220
Tridens flavus (L.) Hitch., 8345
Tridens strictus (Nutt.) Nash, 8343, 8346
Polemoniaceae
Phlox pilosa L., 8184
Polygalaceae
Polygala verticillata L., 8199
Portulacaceae
Claytonia virginica L., 8143
Rosaceae
Crataegus spathulata Michx.
Rubus argutus Link
Rubus trivialis Michx., 8306
Rubiaceae
Diodia teres Walter, 8337
Galium obtusum Bigelow, 8196
Galium pilosum Aiton, 8257
Houstonia pusilla Schöepf
Scrophulariaceae
Agalinis tenuifolia (Vahl) Shinners, 8353
Aureolaria grandiflora (Benth.) Pennell, 8335
Pedicularis canadensis L., 8148, 8192
Penstemon laxiflorus Pennell, 8285
Smilacaceae
Smilax bona-nox L.
Smilax glauca Walt., 8261, 8289, 8320
Smilax smallii Morong, 8319
Ulmaceae
Ulmus alata Michx., 8300, 8378
Verbenaceae
Callicarpa americana L., 8268
Violaceae
Viola pedata L., 8138
Vitaceae
Parthenocissus quinquefolia (L.) Planch.
Vitis rotundifolia Michx., 8264

National Forest sample, 158 species; Sabine National Forest sample, 196 species) these figures indicate that all three are probably the same or very similar communities. Van Kley and Welch (2003), in a study using multivariate ordination and classification of 420 sites across the West Gulf Coastal Plain including shortleaf pine/oak-hickory forest and upland longleaf pine forest/savanna, found that plant communities are very similar throughout the region. Carr (2000) found that shortleaf pine/oak-hickory forest resembled pine savanna elsewhere in the southeast United States and pointed out that southeastern pine savanna communities may not be most appropriately defined by dominant overstory species; rather, the hundreds of other plant species present may provide a much better designation of community types. The conclusions of both Carr and Van Kley are reinforced by our finding that none of the species in our shortleaf pine/oak-hickory forest study site is restricted to the Upper West Gulf Coastal Plain.

Other similarities between upland longleaf pine forest/savanna and shortleaf pine/oak-hickory forest are also interesting. The three families that dominate the Barksdale AFB shortleaf pine/oak-hickory forest study area—Asteraceae, Fabaceae, and Poaceae—also dominate the upland longleaf pine forest/savanna in both the Kisatchie National Forest and the Sabine National Forest and account for 43 percent and 42 percent of the flora, respectively (Barksdale AFB shortleaf forest is 46 percent) (MacRoberts et al. 2002; Philipps et al. 2007). Also, shortleaf pine/oak-hickory forest species richness is similar to upland longleaf pine forest/savanna in both the Kisatchie National Forest, which averaged 100 species (range 82–113 species) in four 0.1 ha plots (MacRoberts et al. 2002), and the Sabine National Forest, which averaged 82 species (range 71–112 species) in eight 0.1 ha plots, 29 species (range 17–46) in sixteen 0.001 ha plots, and 12 species (range 5–25) in sixteen 0.0001 ha plots. Finally, the soils in upland longleaf pine forest/savanna and shortleaf pine/oak-hickory forest are similar (MacRoberts et al. 2002).

Table 2. Species richness in the two plots.

Plot and plot size (ha)	No. of plots	Mean species (range)
Plot A		
0.0001	2	16.5(15–18)
0.001	2	30.0(30–30)
0.1	1	107.0
Plot B		
0.0001	2	18.5(18–19)
0.001	2	30.5(28–33)
0.1	1	92.0

Table 3. Soil sample results for the two plots.

Sample (ppm)	pH	Calcium	Copper	Magnesium	Phosphorous	Potassium	Sodium	Sulfur	Zinc	Soil Texture
Plot A	5.35	275.05	0.27	72.80	4.83	73.93	5.78	5.26	0.74	sandy loam
Plot B	5.24	222.69	0.20	45.63	25.01	38.48	4.74	4.86	0.65	fine sandy loam

ACKNOWLEDGMENTS

Bruce Holland, Natural Resources Manager, Barksdale AFB, and Matthew Stroupe, Forester, Barksdale AFB, aided with the study. Charles Allen and Barney Lipscomb made several comments that aided the paper.

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A REVISION TO THE VASCULAR FLORA OF CALCASIEU PARISH, LOUISIANA

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ABSTRACT

The publication of vascular flora surveys of Calcasieu Parish, Louisiana by Neyland et al. in 2000 and Neyland in 2002 are updated and revised. Subsequent field and herbarium research has yielded the discovery of 22 new species for the parish. Additionally, 17 species that previously had been reported by other sources to occur in the parish but were not found in other herbaria or during the two previous surveys have been discovered. Two corrections from the original surveys are also noted.

RESUMEN

Se actualizan y revisan las publicaciones de estudios de flora vascular de la parroquia de Calcasieu, Luisiana por Neyland y otros en 2000 y Neyland en 2002. La investigación subsiguiente de campo y herbario ha resultado en el descubrimiento de 22 nuevas especies para la parroquia. Además, se han descubierto 17 especies que habían sido señaladas por otras fuentes en la parroquia pero que no fueron encontradas previamente en otros herbarios o en los dos estudios anteriores. También se hacen dos correcciones de los estudios originales.

This paper updates and revises the original vascular flora surveys of Calcasieu Parish, Louisiana by Neyland et al. (2000) and Neyland (2002). Specifically, the purpose of this paper is to list new collections from the parish, to list newly discovered specimens that previously were reported from the parish but were unverified and to correct identification errors.

METHODS

Since the publication of the original surveys by Neyland et al. (2000) and Neyland (2002), plant collections from Calcasieu Parish have continued. Voucher specimens were prepared using standard herbarium practices and are housed at the McNeese State University (MCN) and Louisiana State University (LSU) herbaria. Additionally, specimens from the LSU herbarium have been examined. Nomenclature follows Flora of North America Editorial Committee (1997+) and USDA, NRCS (2008).

RESULTS AND DISCUSSION

The following entries are new additions to the vascular flora of Calcasieu Parish. These taxa have not been reported previously as occurring in the parish. Specimen references follow the same format as in the original survey (Neyland et al. 2000) and in the first update (Neyland 2002). Following the collection data is an abbreviation for the vegetative region where each species typically occurs: prairie (**Pr**); pineland (**Pi**); fresh marsh (**FM**); saline marsh (**SM**); swampland (**S**); bottomland forest (**B**); disturbed sites including ditches, pastures, lawns, roadsides etc. (**D**).

Acanthaceae
Ruellia nudiflora (Engelm. & A. Gray) Urb.—*R. Neyland 2238* (MCN) D

Asclepiadaceae
Asclepias tuberosa L. ssp. *interior* Woodson—*R. Neyland 2288* (MCN) B, D, Pi

Brassicaceae
Cardamine hirsuta L.—*R. Neyland 2262* (MCN) D

Burmanniaceae
Burmannia capitata (Walt. ex J.F. Gmel.) Mart.—*R. Neyland 2099* (MCN) Pi

Caryophyllaceae
Stellaria cuspidata Willd. ex Schltdl. ssp. *prostrata* (Baldwin) J.K. Morton—*R. Neyland 2264* (MCN) D

Clusiaceae
Hypericum galioides Lam.—*R. Neyland 780* (LSU) B, S

Commelinaceae
Murdannia nudiflora (L.) Brenan—*R. Neyland 2105* (MCN) D

Cyperaceae
Kyllinga brevifolia Rottb. *R Neyland 913* (LSU) D

Euphorbiaceae
Euphorbia cyathophora Murr.—*R. Neyland 2198* (MCN) D

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Fabiaceae
Medicago sativa L.—*R. Neyland 2106* (MCN) D
Melilotus officinalis (L.) Lam.—*R. Neyland 2097* (MCN) D
Vicia sativa L.—*R. Neyland 2278* (MCN) D
Iridaceae
Iris giganticaerulea Small—*R. Neyland 2249* (MCN) FM, S
Sisyrinchium albidum Raf.—*R. Neyland* 1202 (LSU) D, Pr
Lemnaceae
Wolffiella gladiata (Hegelm.) Hegelm.—*R. Neyland 2377* (MCN) D, FM, S
Orchidaceae
Zeuxine strateumatica (L.) Sthltr.—*R. Neyland 2266* (MCN) D
Poaceae
Panicum hemitomon Schut.—*R. Neyland 2163* (MCN) D, FM
Polygonaceae
Rumex altissimus Alph. Wood—*R. Neyland 2289* (MCN) D, S
Rubiaceae
Oldenlandia corymbosa L.—*R. Neyland 2252* (MCN) D
Richardia scabra L.—*R. Neyland 2239* (MCN) D
Solanaceae
Physalis cordata Mill.—*R. Neyland 2196* (MCN) D
Violaceae
Viola sororia Willd.—*R. Neyland 2263* (MCN) B

The following entries previously have been reported in the parish but were neither collected in the previous two studies (Neyland et al. 2000; Neyland 2002) nor discovered in physical searches of the herbaria listed in the original study (Neyland et al. 2000). These entries provide evidence for the existence of previously unverified species reported in Calcasieu Parish (Neyland 2000). The sources for this information are a recent search of the LSU herbarium and from new field collections. Therefore, these taxa are added to the verified total for Calcasieu Parish.

Asteraceae
Echinacea pallida (Nutt.) Nutt.—*C.A. Brown 5871* (LSU) **Pr**
Euthamia graminifolia (L.) Nutt.—*N.M. Gilmore 3457* (LSU) **D**
Cyperaceae
Carex leptalea Wahlenb. ssp. *harperi* (Fernald) W. Stone—*A. Featherman s.n.* (LSU) **S**
Euphorbiaceae
Chamaesyce prostrata (Aiton) Small—*P. Pias & R.D. Thomas 4477* (LSU) **D**
Croton lindheimerianus Scheele—*P. Pias & R.D. Thomas 4483* (LSU) **D**
Fabiaceae
Baptisia nuttalliana Small—*A. Featherman s.n.* (LSU) **D**
Gentianaceae
Sabatia angularis (L.) Pursh—*D.L. Hartnett* 8 (LSU) **D**
Lamiaceae
Physostegia intermedia (Nutt.) Engelm. & A. Gray—*A. Featherman s.n.* (LSU) **D, FM, Pr**
Lentibulariaceae
Utricularia macrorhiza Leconte—*G.N. Montz 6191* (LSU) **FM, S**
Loganiaceae
Spigelia marilandica (L.) L.—*R. Neyland 2268* (MCN) **B**
Nyctaginaceae
Boerhavia diffusa L.—*P. Pias 4489* (LSU) **D**
Poaceae
Aristida ramosissima Engelm. ex A. Gray—*C. Brown 8641* (LSU) **D, Pr**
Eragrostis elliottii S. Watson—*N.M. Gilmore s.n.* (LSU) **D, Pr**
Rubiaceae
Houstonia purpurea L. var. *purpurea*—*A. Featherman s.n.* (LSU) **B**
Solanaceae
Solanum americanum Mill.—*R. Neyland 1431* (LSU) **D, Pr**
Solanum elaeagnifolium Cav.—*E.C. Wurzlow s.n.* (LSU) **D**
Urticaceae
Parietaria pensylvanica Muhl. ex Willd. *G.N. Montz 3030* (LSU) **D**

The following entries were misidentified in the two previous surveys.
1. The specimen reported as *Nepeta cataria* L. *Walker s.n.* (MCN) **D** is *Stachys floridana* Shuttlw. ex Benth. Therefore, this taxon is removed from the survey.
2. The specimen reported as *Tamarix ramosissima* Ledeb.—*R. Neyland 1303* (MCN) **SM** is *Tamarix gallica* L.

The most notable addition to the flora of Calcasieu Parish is the discovery of a healthy population of *Zeuxine strateumatica* on the campus of McNeese State University. According to the range map published by the Flora of North America Committee (2002), the range of this species extends from Florida and southern Georgia westward to southeastern Louisiana. Therefore, the present collection of *Z. strateumatica* in Calcasieu Parish represents a westward range extension of about 200 km Additional evidence of this westward movement is supplied by Diggs et al. (2006) who reported that *Z. strateumatica* occurs in Harris and Brazos counties in eastern Texas.

As a result of these revisions to the two previous vascular surveys of Calcasieu Parish, the number of

confirmed specific and subspecific entries for the parish is increased to 1,178. The number of reported but unverified entries for the parish is reduced to 113.

ACKNOWLEDGMENTS

I thank Diane Ferguson from the Louisiana State University herbarium for her assistance and Christopher S. Reid and Charles M. Allen who provided helpful reviews.

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BOOK NOTICE

William K. Chapman, Valerie Conley Chapman, Alan E. Bessette, and Arleen Rainis Bessette, with botanical drawings by Philippa Brown. 2008. **Wildflowers of Massachusetts, Connecticut, and Rhode Island in Color.** (ISBN: 978-0-8156-3185-9, hbk.; 978-0-8156-0926-1, pbk). Syracuse University Press, 621 Skytop Road, Suite 110, Syracuse, New York 13244-5290, U.S.A. (**Orders:** www.SyracuseUniversity-Press.syr.edu, email supress@syr.edu, 1-800-365-8929, 1-866-536-4771 fax). $59.95 hbk., $24.95 pbk., 182 pp., 6" × 9".

From the publisher website.—This field guide will give nature enthusiasts instant access to the diverse and beautiful flora of these New England states. Combining 400 color photographs with concise descriptions, it is written in easy-to-follow nontechnical language. Color illustrations have been carefully selected for their scientific accuracy and their aesthetic quality.

Comprehensive in scope, this guide book offers descriptions of commonly encountered, rare, and even protected species not seen in other guides. The authors provide keys to each species based on observable characteristics of color, flower shape, and leaf arrangement, allowing novices and experts alike to quickly identify flowers. Nomenclature has been updated to reflect current and correct usage.

J. Bot. Res. Inst. Texas 3(1): 378. 2009

ADDITIONS AND EMENDATIONS TO THE VASCULAR FLORA OF CADDO PARISH, LOUISIANA

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ABSTRACT

The vascular flora of Caddo Parish, Louisiana, is updated. Subsequent field and herbarium research has yielded 25 species new to the parish. Six species are deleted from the flora. The total parish count is now 1424 species, of which 1183 are native and 241 are exotic.

RESUMEN

La flora vascular de la parroquia de Caddo, Louisiana, está puesta al día. La investigación subsiguiente de campo y herbario ha producido 25 especies nuevas para la parroquia. Seis especies se eliminan de la flora. El recuento actual es de 1424 especies, de las que 1183 son nativas y 241 son exóticas.

INTRODUCTION

Since the publication of "An updated, annotated vascular flora of Caddo Parish, Louisiana, with notes on regional phytogeography and ecology" (MacRoberts & MacRoberts 2006), plant collecting in Caddo Parish has continued and species new to the parish have been found. Consultation of recent literature has resulted in the addition of one species. Examination of herbarium collections of species reported for the parish has also continued, resulting in a reevaluation of some taxa. These additions and emendations are given below. We do not address nomenclatural changes.

ADDITIONS TO THE CADDO PARISH FLORA

ALISMATACEAE

Sagittaria subulata (L.) Buchenau, *Raymond 2167* LSUS, *Reid 5809* FSU, LSU. Recently reported as new to Louisiana, *Sagittaria subulata* was found on the shoreline of Caddo Lake at Oil City where it was locally abundant (Reid et al. 2008).

APIACEAE

Lilaeopsis carolinensis J.M. Coult & Rose, *Reid 5978* LSU. Known from southern Louisiana, *L. carolinensis* has recently been found on the banks of Cross Lake near Shreveport.

ARACEAE

Pistia stratiotes L., *Raymond 2181* LSUS, *Reid 5976* LSU, *Kalinsky s.n.* LSUS. Water lettuce is spreading in the state and has recently been found in Cross Lake and other sites in Caddo Parish.

ASTERACEAE

Senecio ampullaceus Hook., *Reid 6020 with Faulkner* LSU. Thought to be a Texas endemic (Carr 2002) but recently found in southwestern Arkansas and southeastern Oklahoma (Holmes et al. 2006, Singhurst and Holmes 1998), *Senecio ampullaceus* has recently been collected from xeric sandylands in northern Caddo Parish (Reid et al. 2008).

CALLITRICHACEAE

Callitriche pedunculosa Nutt., *MacRoberts & MacRoberts 7306* LSU, LSUS. This species was collected from a saline prairie in southern Caddo Parish.

CISTACEAE

Lechea san-sabeana (Buckley) Hodgdon, *MacRoberts & MacRoberts 7830* LSU, *7834* LSUS. Previously considered a Texas endemic (Carr 2002; Diggs et al. 2006), *Lechea san-sabeana* has recently been found on pimple mounds in saline prairies in Caddo and De Soto parishes (Reid et al. 2008).

CYPERACEAE

Bolboschoenus robustus (Pursh) Sojak, *Reid 6210 with Sibley* LSU, LSUS. This species was found in marshy open ground in an inlet of Caddo Lake. In Louisiana and Texas, it is mainly a coastal species of salt marshes and saline areas. There is

another collection from northern Louisiana in Claiborne Parish (Thomas & Allen 1993).

Carex alata Torr., *Reid 6492 with Faulkner and Brimer* LSU, SWSL. This species was collected in April 2008 from a shrubby marsh, perhaps influenced by beaver, in northern Caddo Parish, where it was growing with abundant *Osmunda regalis* and *Morella cerifera*.

Carex aureolensis Steud., *MacRoberts 1243* and *1281* LSUS, *Haynes 5322* LSU. Collections of *C. frankii* at LSU and LSUS key to this recently described entity (Ford & Reznicek 2002).

Carex bushii Mack., *MacRoberts & MacRoberts 7389* LSU. This species was collected from a saline prairie in southern Caddo Parish and was initially identified as *Carex caroliniana* Schwein.

Eleocharis tenuis (Willd.) Schult., *MacRoberts & MacRoberts 7338* LSU, LSUS. *Eleocharis tenuis* was found in a saline prairie in southern Caddo Parish.

Eleocharis wolfii A. Gray, *Reid 6083* LSUS. *Eleocharis wolfii* is on both the Louisiana rare species list (Louisiana Natural Heritage Program 2009) and Texas list of species-of-concern (Diggs et al. 2006). *Eleocharis wolfii* was collected from wet depressions in a saline prairie in southern Caddo Parish.

Lipocarpha drummondii (Nees) G.C. Tucker, *Thieret 32137* NCU. This species is reported new to Louisiana by Sorrie and LeBlond (2008) based on a Caddo Parish specimen.

Rhynchospora globularis (Chapm.) Small, *MacRoberts & MacRoberts 7428* LSU, LSUS. *Rhynchospora globularis* was found in a saline prairie in southern Caddo Parish.

Scleria muehlenbergii Steud., *Reid 6741* LSU, LSUS. This species was collected from an open seepage area within a power line right-of-way near Mira in northern Caddo Parish.

GENTIANACEAE

Bartonia paniculata (Michx.) Muhl., *Reid 4638* LSU, TEX-LL, *Reid 6405 with Witsell* LSUS. Specimens cited here were collected from the same locality, a forested seep in northern Caddo Parish. Collected in August 2003, *Reid 4638* is referable to *Bartonia paniculata* subsp. *texana* (Correll) K. Mathews, Dunne, E. York, & Struwe, stat. nov. (Mathews et al. 2009). This specimen was determined as *B. texana* Correll (then recognized as a distinct species) by the collector, and a duplicate sent to TEX-LL was annotated by Jason Singhurst as *B. texana*. *Bartonia paniculata* subsp. *texana* is included in Caddo Parish by Mathews et al. (2009) on the basis of the *Reid 4638* specimen at TEX-LL. Collected in October 2007, *Reid 6405* is intermediate between the descriptions of *B. texana* and *B. paniculata* (Correll & Johnston 1970). *Bartonia paniculata* subsp. *paniculata* is expected in Caddo Parish.

HYDROCHARITACEAE

Hydrilla verticillata (L.f.) Royle, *MacRoberts & MacRoberts 7464b* LSUS, *Kalinsky s.n.* LSUS. *Hydrilla verticillata* recently reached Caddo Parish, where it has now spread to many lakes and ponds.

LENTIBULARIACEAE

Utricularia purpurea Walt., *Raymond 2165* LSUS, *Reid 5800* LSU. Purple bladderwort was found recently to be abundant in Black Bayou Lake at Noah Tyson Park in northern Caddo Parish. This species occurs in coastal areas of Louisiana and Texas and must be a recent arrival to Caddo Parish since Noah Tyson Park is a frequent stop for botanists and the species would have been noticed if it were a long-standing resident.

Utricularia radiata Small, *Reid 6488 with Faulkner and Brimer* LSU. This bladderwort is an aquatic and was found in a beaver-influenced slough dominated by *Nyssa aquatica* in northern Caddo Parish.

Utricularia subulata L., *Reid 6486 with Faulkner* LSU. This species was recently discovered in an open, sandy seep along a stream bisecting a power line right-of-way near Mira in northern Caddo Parish.

LYCOPODIACEAE

Lycopodiella appressa (Chapm.) Cranfill, *MacRoberts & MacRoberts 8334* LSUS. Southern clubmoss was found to be locally common in a small seepage area within a power line right-of-way near Mira in northern Caddo Parish.

NAJADACEAE

Najas minor All., *Kalinsky s.n.* LSUS. This species was recently found on the shoreline of Cross Lake. It is an Old World introduction that is scattered in Louisiana, mostly in the northern part of the state; it is not yet known for East Texas but is expected (Diggs et al. 2006).

SALVINACEAE

Salvinia molesta D.S. Mitch., *Reid 5798 with Jones* LSU, LSUS, *Kalinsky s.n.* LSUS. This is another invasive aquatic plant that apparently reached Caddo Parish very recently, where it was found growing abundantly in Caddo Lake. Since its discovery in the parish in May 2006, it has spread within Caddo Lake and has appeared in Cross Lake (C. Reid, pers. obs.).

XYRIDACEAE

Xyris difformis (Chapm.) var. *difformis*, *Reid 6745, 6746* LSU; *6747, 6749* LSUS. This species occurs in an open seepage area within a power line right-of-way near Mira in northern Caddo Parish.

Xyris laxifolia Mart. var. *iridifolia* (Chapm.) Kral, *Barbour 1099* LSUS. We had previously identified this as *X. caroliniana* Walt.

EXCLUDED FROM THE CADDO PARISH FLORA

ASTERACEAE

Solidago ulmifolia Muhl. ex Willd. is *S. rugosa* P. Mill.

BRASSICACEAE

Cardamine pensylvanica Muhl. ex Willd. is *C. parviflora* L.

CYPERACEAE

Carex frankii Kunth. See *Carex aureolensis* in Additions list.

Carex caroliniana. See Carex bushii in Additions list.

Websteria confervoides (Poir.) Hooper. Like others before us,

we misidentified a sterile aquatic species of *Eleocharis* as *Websteria*. Although widely reported from Louisiana (Thomas & Allen 1993), this species probably does not occur in the state (Bruhl 2002).

XYRIDACEAE

Xyris caroliniana Walt. See *Xyris laxifolia* Mart. var. *iridifolia* (Chapm.) Kral under Additions.

NOMENCLATURAL ERROR

CHENOPODIACEAE

Bassia scoparia should be *Kochia scoparia* (L.) Schroder.

DISCUSSION

The Caddo Parish vascular plant count now stands at 1424, of which 1183 are native and 241 are exotic. By Florida standards, Caddo Parish is well collected and exceeds predicted species richness (Williams & Debilica 2008).

ACKNOWLEDGMENTS

We thank George Dickson and Ralph and Becky Dalton for allowing our surveys on Dickson and Dalton saline prairies, respectively. Sidney Evans and James Taylor allowed us to survey Barron Road Prairie in Caddo Parish. We thank D.W. and Patricia Little for allowing access to their property to collect *Senecio ampullaceus*. Ryan Hook allowed access to the *Senecio ampullaceus* location through his family's property and we appreciate his kindness and interest. Jason Singhurst verified our first collection of *Lechea san-sabeana*. We thank Robert Haynes for verifying a duplicate of *Sagittaria subulata*. Charles Bryson (SWSL) vetted a number of *Carex*. We thank Craig Windham of Caddo Levee District for allowing access to Levee District lands. We are indebted to Sam Brimer, Forester with Caddo Levee District, for taking us to Levee District lands in north Caddo Parish. We thank Alan Boyd, Weyerhaeuser Company, for allowing access to the seep with *Lycopodiella appressa*, *Utricularia subulata*, and others. Deltic Timber Company allowed access to some of their lands in north Caddo. Larry Raymond facilitated access to Caddo Parish parks. The Nature Conservancy allowed access to Caddo Black Bayou Preserve near Rodessa. Royal Tyler kindly hosted us on his property near Rodessa. Charles Allen reviewed the paper.

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MENTHA SUAVEOLENS AND *M.* ×*ROTUNDIFOLIA* IN NORTH CAROLINA: A CLARIFICATION OF DISTRIBUTION AND TAXONOMIC IDENTITY

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ABSTRACT

A clarification of the distribution and identity of *Mentha suaveolens* and *Mentha* ×*rotundifolia* is presented. Naturalized populations of *M.* ×*rotundifolia* are reported from North Carolina for the first time. Previous reports of *M.* ×*rotundifolia* were based on misapplication of the non-hybrid name *M. rotundifolia* to *M. suaveolens*. *Mentha* ×*rotundifolia* is now known to be well established in northwestern North Carolina and several new populations are documented. A population of *M. suaveolens* is also reported for the first time since 1970. This species is apparently scattered and uncommon in North Carolina. Contrary to previous literature reports *M. longifolia* does not appear to be present in North Carolina. A key and photographs are provided to assist in the identification of these taxa.

RESUMEN

Esta investigación presenta una clarificación de la distribución e identidad de *Mentha suaveolens* y *Mentha* ×*rotundifolia*. Se encuentran poblaciones naturalizadas de *M.* ×*rotundifolia* en Carolina del Norte por la primera vez. Las citas anteriores de *M.* ×*rotundifolia* estaban relacionados con una equivocación en la clasificación del nombre *M. rotundifolia* con *M. suaveolens*. *Mentha* ×*rotundifolia* se encuentra muy bien establecida en el noroeste de Carolina del Norte y este estudio documenta varias poblaciones nuevas. Por la primera vez desde 1970, se identifica una población nueva de *M. suaveolens*. Esta especie aparece muy dispersa en Carolina del Norte. Al contrario de publicaciones anteriores, *M. longifolia* no aparece en Carolina del Norte. Se incluyen una leyenda y fotos para apoyar la identificación de estos taxa.

INTRODUCTION

The genus *Mentha* has traditionally been regarded as taxonomically difficult. High levels of morphologic plasticity within this group have been attributed to rampant hybridization, polyploidy, colonial mutant propagation, and the persistent/spreading nature of nothomorphs (Stace 1997; Tucker & Chambers 2002; Bunsawat et al. 2004). In addition, the genus *Mentha* is extensively cultivated for its economic value (e.g., culinary use, essential oil production, ornamental value) (Mabberley 1997; Sutour et al. 2008). As a result of such hybridization and the continued human introduction of multiple taxa, misidentification and uncertainty in the literature is expected.

The primary purpose of this paper is to clarify the distribution and taxonomic identity of what has traditionally been referred to as *Mentha rotundifolia* auct. non. (L.) Huds. in North Carolina. It is beyond the scope of this paper to address all the taxa within the genus *Mentha*. Rather, we will focus on the state-wide distribution and confusion of a single taxonomic concept that has been traditionally misapplied in this state and elsewhere. The information presented will also assist in the identification of *Mentha* specimens in other geographic areas where the concept of *M. rotundifolia* has been applied.

THE PROBLEM

While collecting in northwestern North Carolina we encountered a confounding member of the genus *Mentha* at a several scattered localities. All of these specimens had terminal inflorescences and pubescent, rugose leaves. These plants most closely matched the concepts of *M. rotundifolia* and *M. longifolia* (L.) L. in the *Manual of the Vascular Flora of the Carolinas* (Radford et al. 1968) and the concept of *M. suaveolens* Ehrh. in the *Flora of the Carolinas, Virginia, and Georgia, northern Florida, and surrounding areas* (Weakley 2008). *Mentha*

rotundifolia is now considered to be a hybrid derived from a cross between *M. longifolia* and *M. suaveolens* and is referred to as *M.* ×*rotundifolia* (L.) Huds. (Tucker & Naczi 2007). The name *M. rotundifolia* has been misapplied to *M. suaveolens*, *M.* ×*rotundifolia* and *M.* ×*villosa* Huds. on herbarium sheets, in the literature, and in the herb trade (A.O. Tucker, pers. comm.). In addition, *M. rotundifolia* has been erroneously considered synonymous with *M. suaveolens* by some authors (e.g., Sutour et al. 2008).

Mentha longifolia, M. suaveolens and *M.* ×*rotundifolia* have all been considered infrequent escapes in North Carolina and are only reported from a few counties (Wofford 1989; Radford et al. 1968; USDA, NRCS 2009). The *Mentha* we encountered has apparently become well established outside of cultivation in Alleghany, Ashe and Watauga counties. For this reason we set out to clarify the identity of these plants and to determine where they had previously been documented in North Carolina.

METHODS

In addition to our own field collections, we requested all specimens labeled as *M.* ×*rotundifolia, M. suaveolens, M. longifolia*, including relevant synonyms, as well as *Mentha* specimens not identified below genus from all major North Carolina herbaria. Additionally, we requested loans of the type specimens of *M. suaveolens* and *M. spicata* L. var. *rotundifolia* L. from GOET and UPS respectively. Tucker and Naczi (2007) was used for identifying basionyms and locating the institutional repositories for the type specimens. Specimens were examined from the following herbaria: BOON, DUKE, NCSC, NCU, UNCC, WCU, and WNC. All herbarium acronyms follow Index Herbariorum (Holmgren & Holmgren 1998). High resolution digital photos of the lectotype specimens of *M. suaveolens* and *M. spicata var. rotundifolia* were also examined. In all, we examined 10 vouchers and respective duplicates of *M.* ×*rotundifolia* and 12 of *M. suaveolens* from North Carolina. In addition, we examined many vouchers of cultivated *Mentha* hybrids from the herbarium of M.J. Murray supplied by A.O. Tucker.

RESULTS

The examination of type specimens and previously published literature (e.g., Stace 1997; Tucker & Naczi 2007), revealed 11 vouchers of *M. suaveolens* and one previous collection of *M.* ×*rotundifolia* from North Carolina. No specimens of *M. longifolia* were seen. Our own field work in northwestern North Carolina located 9 new populations of *M.* ×*rotundifolia* and one new population of *M. suaveolens* (Fig. 1). Our specimens represent the first known accounts of naturalized populations of *M.* ×*rotundifolia* in North Carolina and the first collections since 1990. Prior to this study, *M. suaveolens* had not been collected since 1970. *Mentha longifolia* has apparently not yet been legitimately documented for North Carolina.

A key, specimen citations, and photographs (Fig. 2) are provided below to facilitate the identification of additional populations of *M.* ×*rotundifolia* or *M. suaveolens*. We include *M. longifolia*, *M. spicata* and *M.* ×*villosa* in the key because they have been confused with *M.* ×*rotundifolia* or *M. suaveolens* in the past. *Mentha longifolia* and *M.* ×*villosa* have not been documented from North Carolina; however, these taxa have been reported from the eastern United States (e.g., Rhoads & Block 2007; Weakley 2008, Tucker in press). We therefore include these taxa in the key to increase its utility. Most of the specimens examined were readily identifiable as either *M.* ×*rotundifolia* or *M. suaveolens*. However, some specimens had primary affinities with *M. suaveolens*, but exhibited some intermediacy. As pointed out by Stace (1997), these intermediate taxa are usually hybrids involving *M. suaveolens* and can be difficult to distinguish. However, the following key can be reliably used to separate *M.* ×*rotundifolia* and *M. suaveolens* for a great majority of specimens. Back crosses between *M.* ×*rotundifolia* and it parents have been documented in common garden settings, though it is not clear if this occurs in naturalized populations. The taxa included in the key can be distinguished from other *Mentha* taxa in North Carolina by the presence of a terminal spike with densely crowded flowers. It should be noted that 3 subsp. of *M. suaveolens* have been recognized by Tucker and Naczi (2007). In addition to the type subsp. these authors recognized subsp. *insularis* (Req.) Greuter and subsp. *timija* (Coss. ex Briq.) Harley ex Harley & Brighton. However, neither a key nor a description is presented by Tucker and Naczi

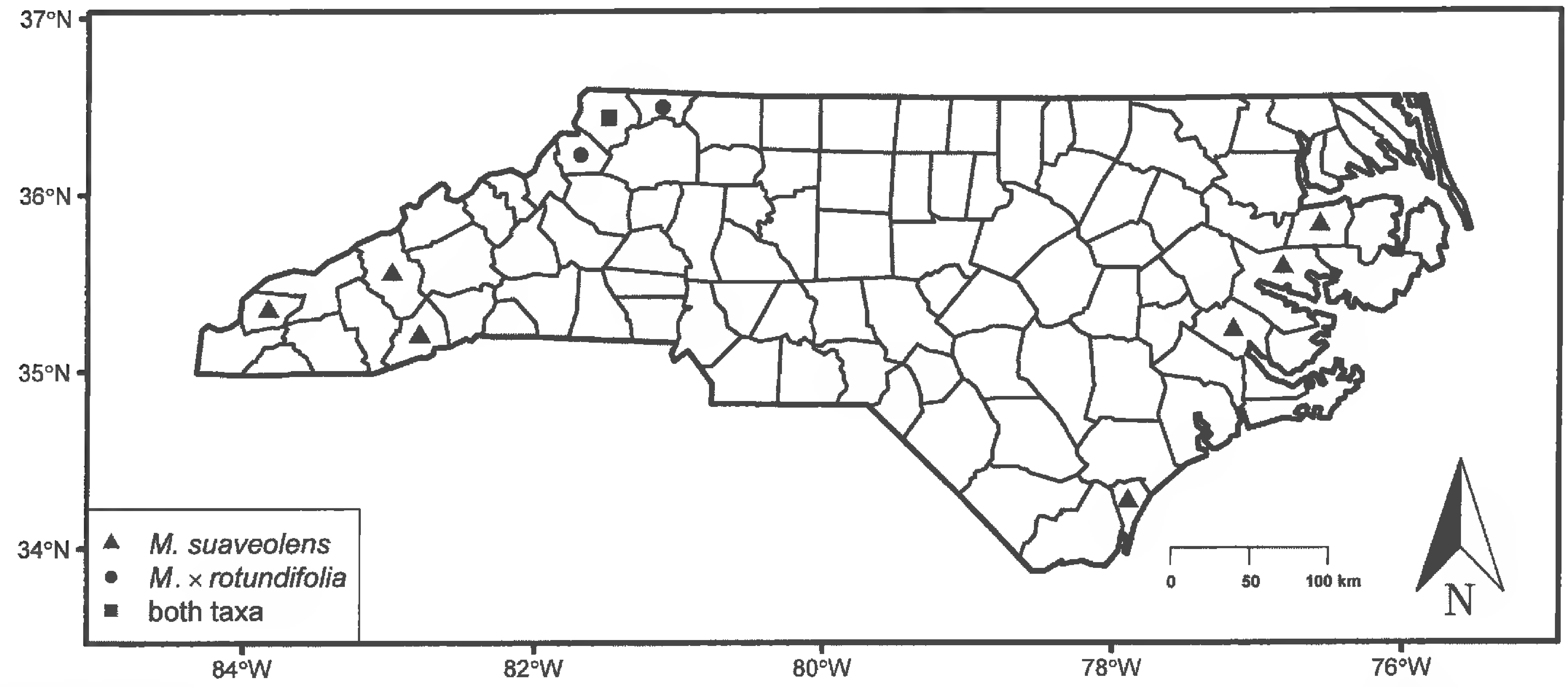

Fig. 1. County level distribution of *M. suaveolens* and *M. ×rotundifolia* in North Carolina (based on specimens from BOON, DUKE, NCSC, NCU, UNCC, WCU and WNC). Symbols are mapped on county centroids.

(2007) to separate these 3 taxa. Harley (1972) expresses doubt as to the distinctiveness of *M. insularis* Req. (= *M. suaveolens* subsp. *insularis*), while subsp. *timija* is not mentioned by Harley since it is outside the geographic scope of this treatment. In short, it is difficult at this time to definitively identify which subsp. of *M. suaveolens* is present in North Carolina, but after a review of existing literature, we have tentatively defaulted with Weakley's (2008) recognition of ssp. *suaveolens*. Future taxonomic studies across the native and introduced ranges of *M. suaveolens* are needed to define these taxa.

KEY TO SELECTED TAXA OF *MENTHA*

Key adapted from Stace (1997), Tucker and Naczi (2007), Weakley (2008) and Tucker (in press). Note: Taxa included within brackets are not currently known from North Carolina.

1. Leaves lanceolate to oblong-lanceolate
   2. Abaxial leaf hairs unbranched, leaves widest near the middle, slightly rugose; fertile anthers 0.28–0.38 mm long, generally musty-odored ($2n = 24$) ______ **[M. longifolia]**
   2. Leaves oblong-lanceolate, adaxially glabrous, rarely with tree-like hairs on undersurface, leaves widest near base, conspicuously rugose; fertile anthers 0.38–0.52 mm, generally spearmint-odored ($2n = 48$) ______ **M. spicata**
1. Leaves oblong to ovate
   3. Leaves generally 1–2× as long as wide, ovate-suborbicular, broadly rounded to subcordate at the base, apex obtuse; leaf serrations rounded and often turned downward (thus appearing somewhat crenate); leaf surface strongly rugose, with scattered dendritic hairs on the abaxial surface; sweet/sickly scented ($2n = 24$) ______ **M. suaveolens**
   3. Leaves generally 1–3× as long as wide, ovate to oblong, broadly cuneate to rounded at the base, apex acute; leaf serrations sharp and patent, leaf surface moderately rugose; spearmint scented.
      4. Leaves generally oblong, with nearly parallel sides and a broad rounded base; each flower generally with 4 fertile anthers ($2n = 24$) ______ **M. ×rotundifolia**
      4. Leaves generally ovate, infrequently oblong; scattered fertile anthers sometimes present ($2n = 36$) ______ **[M. ×villosa]**

Voucher specimens for ***Mentha ×rotundifolia*: NORTH CAROLINA. Alleghany Co.:** Glade Valley, located along US 21 S, ca. 1 mi past Glade Valley Rd., latitude 36.4651, longitude -81.0502, 28 Aug 2008, *Poindexter 08-983* (BOON). **Ashe Co.:** ca. 1.25 mi down William T. Calloway Road, near Bluff Mountain Gameland, latitude 36.3684, longitude -81.5738, 22 Sep 2007, *Zgieb s.n.* (BOON); Orion, located along NC 88/16, ca. 1 mi from 16 S divergence and the South Fork of the New River, traveling E just past Frank Dillard Rd., latitude 36.3956, longitude -81.4185, 28 Aug 2008, *Poindexter 08-993* (BOON). West Jefferson, located at the base of Mount Jefferson, at the jct. of Oakwood Rd. and Cottontail Trail, latitude 36.3878, longitude -81.4663, 7 Aug 2008, *Poindexter 08-673* (BOON). West Jefferson, located

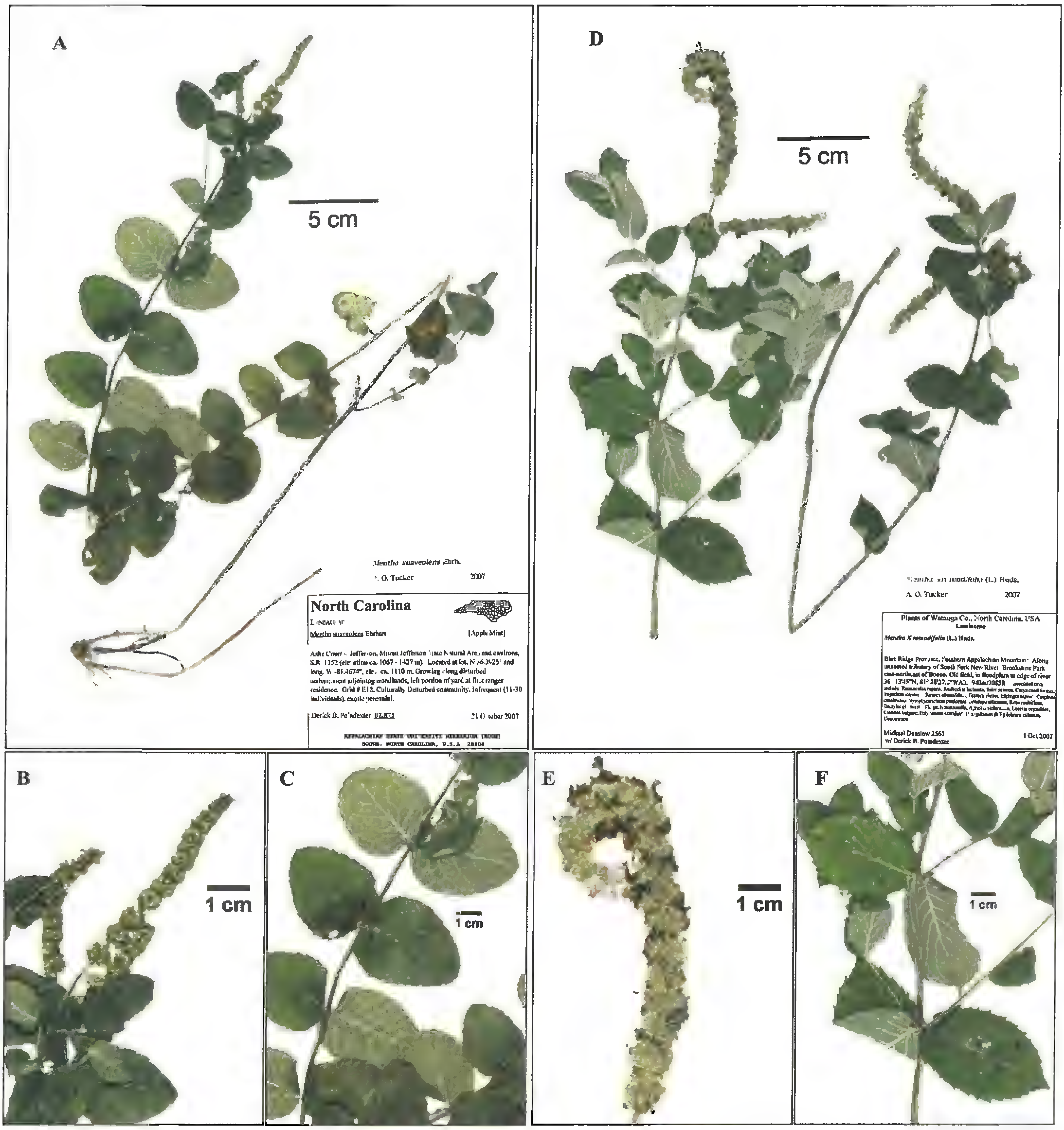

Fig. 2. Specimen, leaves, and inflorescences of A–C) *Mentha suaveolens*, and D–F) *Mentha* ×*rotundifolia*.

along Mount Jefferson Rd., ca. 1 mi prior to Ashe County High School and past Oakwood Rd., latitude 36.3858, longitude -81.4804, 7 Aug 2008, *Poindexter 08-674* (BOON). **Watauga Co.:** below Boone, beside a large creek off US 421; a dirt Rd., 15 Sep 1990, *Basinger 853* (UNCC); Boone, near US 421 bridge on Charlie Hollar Rd., ruderal embankment of the South Fork of the New River, latitude 36.2203, longitude -81.6399, 22 Oct 2005, *Poindexter 05-2255* (BOON, DOV); Greenway Trail E of Boone, along unnamed tributary of South Fork New River, latitude 36.2114, longitude -81.6478, 18 Sep 2007, *Denslow 2560* (BOON, DOV); along unnamed tributary of South Fork New River, Brookshire Park ENE of Boone, latitude 36.2292, longitude -81.6411, 1 Oct 2007, *Denslow & Poindexter 2561* (BOON, DOV); Boone, located along Wilson Rd., just before the jct. with NC 105 (Linville Rd.), latitude 36.2025, longitude -81.6721, 14 Aug 2008, *Poindexter 08-832* (BOON).

Habitat and Phenology.—*Mentha* ×*rotundifolia* has so far been observed in wet depressions, and disturbed areas including floodplains and streambanks. It has been collected between early August and late October,

with a majority of the vouchers made between mid August and late September. The average collection date was the 9th of September.

Voucher specimens for ***Mentha suaveolens*: NORTH CAROLINA. Ashe Co.:** Jefferson, Mount Jefferson State Natural Area and environs, S.R. 1152, growing along disturbed embankment adjoining woodlands, at latitude 36.3925 and longitude -81.4674, 11 Aug 2005, *Poindexter 05-1695* (BOON); same as previous locality, 21 Oct 2007, *Poindexter 07-874* (BOON, DOV). **Beaufort Co.:** Belhaven, Salt marsh, 6 Jul 1958, *Radford 36297* (NCU). **Craven Co.:** New Bern, waste place, 19 Jul 1958, *Radford 37332* (NCU). **Graham Co.:** meadow border, 2.5 mi N of Robbinsville, on [U.S.] 129, 20 Jun 1965, *Crisp s.n.* (WCU). **Haywood Co.:** Creek side, 5.2 mi ENE of Crabtree, 5 Jun 1958, *Ahles & LaDuke 42139* (NCU). **New Hanover Co.:** Wilmington, moist thicket, 7 Jul 1938, *Godfrey 4880* (NCSC); Wilmington. E bank of Cape Fear River off U.S. 421, marshy field, 6 Aug 1966, *Bradley & Stevenson 3395* (BOON, DUKE, NCU, UNCC, WCU, WNC not seen); along railroad tracks on E side of Northeast [Cape Fear] River at US 17, Wilmington, 23 Oct 1968, *Leonard & Radford 2214* (NCU); Wilmington, ballast area, Northeast [Cape Fear] River, 22 Aug 1970, *Leonard 3553* (WCU). **Transylvania Co.:** Cascade Lake, 15 Aug 1958, *Freeman 58312* (NCU). **Washington Co.:** 0.4 mi E of Plymouth, fresh-water marsh, near Roanoke River, 5 Aug 1958, *Radford 38817* (NCU).

Habitat and Phenology.—Mentha suaveolens is primarily restricted to moist or wet areas such as lake shores, creek sides and salt marshes. It has also been observed in disturbed sites such as along railroads and road embankments. This species has been collected between early June to late October, though a majority of the specimens were vouchered between early July and mid August. The average collection date was the 5th of August.

DISCUSSION

Naturalized populations of *M.* ×*rotundifolia* sensu Tucker and Naczi (2007) are reported from North Carolina for the first time. This hybrid has been reported from North Carolina previously (e.g., USDA, NRCS 2009); however, as stated above, these reports were apparently based on misapplication of the name *M. rotundifolia* to *M. suaveolens*.

Mentha ×*rotundifolia* is widely cultivated and this is most likely the pathway by which this plant was introduced into North Carolina. Horticulture and agriculture are common vectors of plant introduction to new areas (Reichard & White 2001). *Mentha* ×*rotundifolia* has been cultivated in the Boone area for at least 50 years. We examined a vouchered garden planting of *M.* ×*rotundifolia* dated 1957 from Davidson (Mecklenburg County) that was 'transplanted from Boone, N.C.' [*Brown 689*, 10 July 1957, (UNCC)]. Today, cultivated stems are sold at local farmer's markets in western North Carolina [*Denslow 2591*, 30 Aug 2008, (BOON)]. Regardless of the mode of introduction, this plant is now well established outside of cultivation. Although we have observed naturalized populations in close proximity to cultivated plants, most populations appear to be established in more disparate localities. It is most successful in moist areas near water sources where it can become the dominant plant.

In light of the prevalence of *M.* ×*rotundifolia* in northwestern North Carolina, it is unclear why this plant was only collected once prior to 2007. One possible explanation is that this plant has simply been overlooked by collectors. Another possibility is that *M.* ×*rotundifolia* has only recently become successful outside of cultivation. Long periods from initial establishment to subsequent spread or 'lag times' are commonly observed for introduced species (Lockwood et al. 2007). Explanations for these lag times include an increase in positive biotic interactions and post-establishment evolution that promotes range expansion (Lockwood et al. 2007). It is also possible that the rate of introduction (i.e., propagule pressure, Lockwood et al. 2007) has increased in recent years.

A previous report by Radford et al. (1968) of *M. longifolia* from Gates County, North Carolina was based on a misidentification of *M. spicata*. Radford et al. (1968, p. 924) reports *M. longifolia* as a 'very rare escape' from a 'roadside ditch'. This report is apparently based on a specimen collection by H.E. Ahles on 1 Aug 1958 and is now listed as *M. spicata* in the NCU database (http://www.herbarium.unc.edu/seflora/firstviewer.htm). Thus, *Mentha longifolia* has not yet been collected in North Carolina.

The first report of *M. rotundifolia* for North Carolina appears to be from the Wilmington area (Curtis 1834). Curtis's (1834) description of this plant indicates that it may actually be *M. suaveolens*. Curtis (1834,

p. 26) states that the plants have leaves that are "roundish, rugose, crenate, sessile" and are "unpleasantly scented." These characters are consistent with *M. suaveolens*, though voucher specimens for this report have not yet been located.

Radford et al. (1968) apparently misapplied the name *M. rotundifolia* to specimens of *M. suaveolens*. This misapplication may have caused other authors (e.g., NRCS-USDA 2009; Weakley 2008) to incorrectly report *M.* × *rotundifolia* from North Carolina. Contrary to these reports we examined no previous specimens labeled *M.* × *rotundifolia* from North Carolina. We did however locate a specimen of *M.* × *rotundifolia* collected in 1990 [*Basinger 853*, (UNCC)] that was misidentified as *M. spicata*. This specimen seems to be the first known collection of *M.* × *rotundifolia* from North Carolina.

Based on current herbarium records, *M. suaveolens* appears to infrequently establish in North Carolina. It is possible however that this taxon is more frequent, but has been overlooked by collectors. Future plant collecting and detailed habitat descriptions will help determine if this plant persists at the historic sites where is has been documented. In particular, *M. suaveolens* should be sought in the Wilmington area where it was collected several times in the past.

ACKNOWLEDGMENTS

We extend our appreciation to the curators and staff of DUKE, NCSC, NCU, UNCC, WCU, and WNC for access to their specimens, as well as GOET and UPS for images of type specimens. We would like to thank Arthur O. Tucker for verification of our original specimens, for generously providing specimens of *Mentha* hybrids and valuable insights that improved the manuscript. We are especially grateful for the helpful suggestions on this manuscript provided by Christine Edwards, Gabrielle Katz and the Spanish translation of the abstract provided by L. Baker Perry. Funds to offset publication costs were graciously provided by the Graduate Student Association Senate at Appalachian State University.

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BOOK NOTICE

Pamela A. Matson and Ashok Gadgil (eds.). 2008. **Annual Review of Environment and Resources, Volume 33.** (ISSN 1543-5938; ISBN 978-0-8243-2333-2, hbk.). Annual Reviews, 4139 El Camino Way, P.O. Box 10139, Palo Alto, California 94303-0139, U.S.A. (**Orders:** www.annualreviews.org, science@annualreviews.org, 800-523-8635, 650-493-4400). $78.00 indiv., 481 pp., cumulative indices, 7 1/2" × 9 3/8".

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CASTILLEJA ANGUSTIFOLIA VAR. *DUBIA* (SCROPHULARIACEAE), A NEW RECORD FOR SOUTH DAKOTA

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ABSTRACT

We report the first documented occurrence of *Castilleja angustifolia* (Nutt.) G. Don var. *dubia* A. Nelson (*C. chromosa* A. Nelson) in South Dakota. The species was found on the Buffalo Gap National Grassland by Lynn Hetlet in 2002 and subsequently collected, identified, and vouchered by Grace Kostel in 2006. Its distribution, salient morphological features, and habitat are discussed.

RESUMEN

Citamos la primera ocurrencia documentada de *Castilleja angustifolia* (Nutt.) G. Don var. *dubia* A. Nelson (*C. chromosa* A. Nelson) en Dakota del Sur. La especie fue encontrada en el Buffalo Gap National Grassland por Lynn Hetlet en 2002 y luego colectada, identificada y comprobada por Grace Kostel in 2006. Se discuten la distribución, los rasgos morfológicos sobresalientes y el hábitat.

INTRODUCTION

The *Artemisia tridentata* Nutt. shrub habitat in southwest South Dakota begins to give way to mixed-grass prairie and represents the extreme eastern edge of *A. tridentata*. Much of the immediate region is under public ownership and administered by the USDA Forest Service Nebraska National Forest. *Castilleja angustifolia* var. *dubia* (*C. chromosa*) is an associate of *A. tridentata* at lower elevations (Holmgren 1984). A floristic inventory of the Buffalo Gap National Grassland and vicinity was conducted recently, and led to the discovery of several other species new to the grassland (Kostel 2006).

Distribution.—*Castilleja angustifolia* var. *dubia* (*C. chromosa* A. Nels.) ranges throughout and peripheral to the Intermountain region, central and eastern Wyoming, western Colorado, northwest New Mexico, central and northern Arizona, and eastern California (Holmgren 1984; Chumley 1996).

Voucher specimen: **U.S.A. SOUTH DAKOTA. Fall River Co.:** T8S R1E S34 N1/2 Mule Creek SE Quad.; 43.3169° N; -103.9876° W (Datum = NAD83 Zone 13); Buffalo Gap National Grassland ca. 8 air mi WNW of Edgemont and ca. 1 mi due N of SD Hwy. 18; *Artemisia* shrub-steppe; one plant with ca. 12 inflorescences, bright yellow; soils are coarse (sand with gravel), permeable, and overlie shale, 20 May 2006, *Grace Kostel 10056* (BHSC, SD, USA).

Morphology.—Perennial herb from woody base, 1–4 dm tall, stems ascending to erect, usually several in a cluster, herbage densely hispid with long, somewhat flat, multicellular hairs; leaves with 3–7 lobes distally; inflorescence often broad and compact, bright red to orange-red, occasionally yellow; bracts lanceolate with 1–3 pairs of rounded segments; calyx 20–27 mm long, the primary lobes 6–12 mm long adaxially, 4–10 mm long abaxially; corolla 20–32 mm long, galea 10–18 mm long, about half the corolla length, the lower lip much reduced with incurved teeth, the tube 10–13 mm long; capsule 9–15 mm (Holmgren 1984; Dorn 2001).

Soil.—The most influential feature affecting vegetation at the site of *C. angustifolia* var. *dubia* is soil. Soils are of the Samsil series characterized by clay, smectitic, calcareous, mesic, shallow, and aridic ustorthent found on gently sloping to very steep hills, ridges, and breaks of dissected shale plains. These soils formed in alluvium or residuum weathered from shale. The loose texture makes it susceptible to localized wind erosion of topsoil when it is grazed too heavily (Soil Survey Staff 1982).

Habitat.—The area supports dry upland shrub communities of *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young, *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird, *Atriplex* spp., and *Sarcobatus*

vermiculatus (Hook.) Torr. These shrubs are interspersed with bare ground and graminoids, e.g., *Bouteloua gracilis* (Willd. ex Kunth) Lab. ex Griffiths, *Bouteloua curtipendula* (Michx.) Torr., *Hesperostipa comata* (Trin. & Rupr.) Barkworth, *Pascopyrum smithii* (Rydb.) Á. Löve, and *Bromus* spp. The forbs *Thermopsis rhombifolia* (Nutt. ex Pursh) Nutt. ex Richardson, *Draba nemorosa* L., *Lesquerella arenosa* (Richardson) Rydb. var. *arenosa*, *Penstemon eriantherus* Pursh, *Oxytropis lambertii* Pursh, *Lepidium densiflorum* Schrad., *Descurainia pinnata* (Walter) Britton, and *Androsace occidentalis* Pursh are associate species at this site. The Buffalo Gap National Grassland is leased for cattle grazing. Additionally, the area is browsed by native fauna including deer, antelope, and small mammals.

DISCUSSION

This is the first report for *C. angustifolia* var. *dubia* in South Dakota. It has conservation status in Montana (S3) and Idaho (S4) and is SNR/SU throughout the remainder of its range (Nature Serve 2008). *Castilleja angustifolia* var. *dubia* is not a rare species when its entire range is considered, and certainly it is not rare in adjacent Wyoming (Chumley 1996); however, its occurrence in southwestern South Dakota is likely due to the unusual habitat.

CONCLUSIONS

Upon review of specimens at BHSC and RM, it is clear that *Castilleja angustifolia* var. *dubia* occurs in southwestern South Dakota on the Buffalo Gap National Grassland in Fall River County. Additional floristic surveys in the area might result in the discovery of additional plants.

ACKNOWLEDGMENTS

The authors wish to thank Ronald L. Hartman, B. Ernie Nelson, Gary E. Larson, Ronald R. Weedon, and Steven B. Rolfsmeier for reviews of the manuscript, and the Rocky Mountain Herbarium (RM) and Black Hills State University Herbarium (BHSC) for the use of specimens for identification and services. Sincere appreciation is extended to Mark L. Gabel for the Spanish translation.

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GLYCERIA DECLINATA (POACEAE) NEW TO THE FLORA OF TEXAS

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ABSTRACT

Glyceria declinata Brébiss (Poaceae) is reported new to Texas and diagnostic features are presented to distinguish it from the other three species of *Glyceria* in that state.

RESUMEN

Glyceria declinata Brébiss (Poaceae) Se cita como nueva para Tejas se presentan las características diagnósticas para diferenciarla de las otras tres especies de *Glyceria* en el estado.

Low glyceria (**Glyceria declinata** Brébiss) (Poaceae) (Fig. 1) is a European species that has become established on the western seaboard of North America from southern British Columbia to southern California (Barkworth & Anderson 2007; Whipple et al 2007)). It is also reported from northeastern Nevada, Arizona, and Long Island, New York. Saichuk et al (1981) reported it new to Louisiana from Jefferson Davis Parish and Allen et al (2004) lists it from nine additional parishes. Three species of *Glyceria* (*G. arkansana* Fern., *G. septentrionalis* A. Hitchc., and *G. striata* (Lam.) A. Hitchc.) are reported for Texas (Diggs et al. 2006; Barkworth

Fig. 1. *Glyceria declinata* Brébiss from Hitchcock (1950: 86, fig. 94).

J. Bot. Res. Inst. Texas 3(1): 393 – 394. 2009

& Anderson 2007; USDA, NRCS 2009), This collection is apparently the first collection of *G. declinata* for Texas. *Glyceria declinata* can be separated from *G. striata* by its erect rigid pedicels, spikelets longer than 5 mm with more than seven florets, and lemmas longer than 2.5 mm compared to weak flexuous pedicles, spikelets shorter than 5 mm with seven florets or fewer, and lemmas shorter than 2.5 mm in *G. striata*. *Glyceria declinata* is a smaller stature plant (shorter than 0.5 m) and has lemma apices that are irregularly lobed compared to tall plants (mostly 1 m and taller) and lemmas with entire to slightly crenate apices in both *G. arkansana* and *G. septentrionalis*.

Voucher specimens: **TEXAS. Newton Co.:** Caney Creek Park, S of Hwy. US 190 in Newton, 30° 50' 842"N 93° 45' 802"W, 17 Mar 2008, *Allen and Lewis 20732* (BRIT, FTPK).

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VEGETATION AREAS OF TEXAS: CONCEPT AND COMMENTARY

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ABSTRACT

Vegetational areas of Texas are based upon a long history of maps developed from the concepts of life forms (physiognomy and structure) and taxa (floristic composition). The number of plant community types in Texas is dependent upon the classification system used and refinements continue. Important results include identification of vegetation types as well as designation of those types that are both threatened and in need of protection. Although boundaries of vegetational areas are difficult to assess, their plant communities are recognizable; thus, the concept of vegetational areas is especially beneficial in floral and faunal conservation and management.

RESUMEN

Las áreas de vegetación de Texas están basadas en una larga historia de mapas desarrollados a partir de conceptos de formas biológicas (fisonomía y estructura) y taxa (composición florística). El número de tipos comunidades vegetales de Texas depende del sistema de clasificación usado y los refinamientos realizados. Los resultados importantes incluyen identificación de los tipos de vegetación así como la designación de aquellos tipos que están amenazados y necesitan protección. Aunque los límites de las áreas de vegetación son difíciles de establecer, sus comunidades vegetales son reconocibles; así, el concepto de áreas de vegetación es especialmente beneficioso en la conservación y manejo de flora y fauna.

INTRODUCTION

MacRoberts and MacRoberts (2008) analyzed the vegetational species richness of Texas. They found that plant species richness does not correlate well with primary productivity or size of currently recognized vegetational areas, i.e., the majority of species are not confined within regional areas. They suggest that the traditional vegetational areas of Texas should be reassessed to provide a simpler vegetational map more reflective of current species distributional information. Therefore, I believe it is important to examine the vegetational area concept; to provide some commentary about the ecological processes that produce these areas; and, to discuss their relevance to conservation and management.

VEGETATIONAL AREAS VS. FLORISTIC AREAS

Landscapes exhibit mosaics of vegetational patterns that relate to life forms (physiognomy and structure) such as trees vs. grasses and taxa (floristic composition, i.e., species pattern), e.g., see Oosting (1956); Dansereau (1957); Küchler (1964); Daubenmire (1968); Shimwell (1971). These patterns are plant communities composed of a limited number of life forms and taxa, some of which are more prominent than others, thus, are recognizable. The presence and proportion of life forms and taxa give a given plant community its recognizable characteristics. Only one life form is usually used to characterize a vegetational unit; but, in some cases different life forms may intersperse such as in a savannah (trees and shrubs dominate in some areas, grasses in others). Changes in floristic composition can be used to subdivide a vegetational area. However, no vegetational scheme of delineation or categorization is universally accepted; thus, vegetational maps based on life forms and taxa are subject to continual interpretation revision, and application (e.g., Gould 1962; Correll & Johnston 1970; McMahan et al. 1984; Diamond et al. 1987; Edwards et al. 1989; Hatch et al. 1990; Bezanson 2000; Diggs & Schultze 2003; Griffith et al. 2004; Telfair 2006). Nevertheless, the concept of vegetational areas is important and necessary for landscape preservation and wildlife habitat conservation and management in Texas (Telfair 1999). See Diggs et al. (2006) for examples of most of these maps in reduced size and color as well as detailed discussion. The Figure 4 map (Telfair's Vegetational Regions of Texas) will require use of a hand lens or magnifying glass to see some county boundaries and to identify small outlier

areas of vegetation. However, the map is available online with a zoom feature—http://artemis.austincollege.edu/acad/bio/gdiggs/EastTX/introduction.pdf—page 6 (p. 23 of the pdf introduction).

Vegetational patterns reflect the influences of many geographic as well as climatic factors that have interacted over long periods of geologic time to produce regions and subregions of characteristic vegetation. In contrast, floristic regions largely reflect only the influence of climatic factors, mainly rainfall and temperature (for comparison, see the 2 maps of vegetational and floristic regions, Turner et al. 2003). However, vegetational patterns are also subject to many widespread human-caused influences, especially farming and ranching, water resource development, forestry practices, mineral and energy production, urban/industrial expansion, recreational/leisure developments, transportation facilities, introduced species, and land fragmentation (USFWS 1979; Gunter & Oelschlaeger 1997; Telfair 1999; James 2000).

COMMENTARY

Texas landscape regions and their included plant communities are more diverse than those of any other state. These regions are defined by their prominent vegetation (vegetation areas) or physiographic features (ecological regions). In most regions, there is close correlation between vegetational and ecological areas except where names refer to physical features, e.g., Coastal Sand Plains, Llano Uplift, Rolling Plains, High Plains, Edwards Plateau, and Trans-Pecos Desertic Basin, Plains, and Mountains. However, most subdivisions within these regions are named for the prominent vegetation therein. These regions are a result of millions of years of the interaction of geological, climatic, and other geographic influences. They form a complex mosaic of odd shapes, sizes, and patterns some of which are interwoven. However, their natural history can be interpreted ecologically.

Spearing (1991) provided maps and analysis of ecological processes that formed the physiography of Texas. Seven basic geologic processes are involved: 1) mountain building and erosion, 2) basin formation and filling, 3) uplifts, 4) volcanism, 5) wind erosion, 6) marine influences, and 7) stream entrenchment. In combination with these geological processes, climatic processes (annual and seasonal rainfall and temperature patterns) produced regional zones that influenced the development of soil associations which, in turn, influenced the types and patterns of vegetation that developed co-regionally (Griffiths & Orton 1968; Godfrey et al. 1973).

The combination of rainfall and temperature patterns, in relation to the influence of topography, forms regional climatic zones of arid to humid, tropical to temperate. Thus, in general, there are 3 major climatic zones in Texas with distinct vegetation: 1) the eastern 10% (humid, forested), central 80% (semi-humid to semi-arid (primarily grasslands and savannahs), and 3) western 10% arid (desert vegetation).The major environmental conditions of these zones are:

Forest.—Major influential environmental factors are precipitation and soil nutrients; fire in some areas (e.g., longleaf pine and post oak savannah communities). Most nutrients are bound in woody tissues for many years, thus, sandy forest soils are especially nutrient deficient.

Grassland.—Major influential environmental factors are drying winds, droughts, irregular rainfall, and lightning-caused fires. Nutrients recycle annually between plants and soils, much being stored in the soil. In relation to rainfall belts, grasses vary from short to tall along a gradient from west to east.

Desert.—Major influential environmental factors are water shortage and heat/cold stress. When deserts formed, local plants adapted and some immigrated from more southern tropical climates.

Other important regional geographic influences are rivers, elevations, soils, and standing water (Spearing 1991). River drainages allow bottomland forests to extend far westward along riparian corridors into grasslands; some smaller drainages also occur in desert areas. The Texas land surface rises gradually from sea level northwestward to almost 1524 m. Abrupt changes in elevation occur at the Balcones and Caprock Escarpments. In the Trans-Pecos Region, mountains rise to heights of 1524–2667 m from valley floors of 914–1219 m elevation. These elevation changes influence regional climates which, in turn, influence the vegetation. Soils are of major influence in the development of growing conditions for vegetation. Worldwide

there are 12 soil orders of which 9 occur in Texas. These 9 orders, in Texas, include 73 soil associations, and about 1300 soil series (National Resource Conservation Service 2008). Thus, the great variety of Texas soils reflects the diversity of geologic, climatic, and biologic conditions during which they developed. Also, there is a strong correlation with vegetational patterns. Soil Order name derivatives (Godfrey et al. 1973; Soil Survey Staff 1999) illustrate the basic soil differences and types of vegetation supported.

Alfisols	Leached of aluminum and iron; subsurface clay accumulation; occur in semiarid to moist areas; primarily in forest areas.
Aridisols	Dry; lack of moisture allows accumulation of salts and minerals; deserts.
Entisols	Recent soils of little development in areas of high erosion or deposition rates; occur in dunes, steep slopes, and flood plains; good examples are Monahans and coastal sand dunes and islands.
Histosols*	High fiber tissue content; mostly saturated bogs and marshes.
Inceptisols	Beginning to moderate development; semiarid to humid slopes; depressions, flood plains.
Mollisols	Soft; dark with accumulated organic matter; highly fertile; grasslands.
Spodosols*	Ash-colored, acid, infertile sandy subsoil with accumulation of iron and organic matter; coniferous forests of humid areas.
Vertisols	High in clays; swell when wet; crack when dry; fairly high in natural fertility; grasslands.
Ultisols	Well-developed, maximum leached; pine forests.

*Occur in small areas; usually too small to map.

Surface water can provide many types of small, local, and diverse plant communities within each vegetation region (e.g., swamps, marshes, oxbow lakes, bogs, seeps, playa lakes).

Some vegetational areas are the result of influencing factors that override or dominate other factors. The Post Oak Savannah (or Clay Pan Savannah) occurs in a forest climate, but developed under the influence of an edaphic factor (a shallow nearly impervious clay pan restricts water percolation during dry periods); so, plant diversity is lessened. An unusual exception to the "Clay Pan" soils occurs in Bastrop County—home of the "Lost Pines", where there is a sandy inclusion of moist soils—the Carrizo Sands—which support a unique community of loblolly pines, a western remnant once connected to the now more eastern pine forest. These relict pines have developed an ecotype more drought-tolerant than those to the east. Blackland Prairies occur in a forest climate, but developed under the control of pyric and edaphic factors. The high clay content of this soil causes it to swell during periods of high rainfall and to shrink during periods of drought. The shrinkage opens wide, deep crack that damage tree roots. Also, most grassland plants are fire-adapted; thus, resprout from below-ground root collars rather than the above-ground terminal buds for most forest plants. The forested areas of the East and West Cross Timbers occur in a grassland climate; but, deep, moist, sandy soil belts allow trees to dominate. Coastal region vegetation is highly variable (dunes, marshes, prairies, and forests). It is influenced by many interacting marine influences (e.g., stream erosion, sedimentation, meandering, and delta formation; wave and tidal action; and the influence of hurricane winds and salt spray. Wind erosion produced the Monahans Sands in west Texas, and the Coastal Sand Plains between Corpus Christi and Brownsville in south Texas.

Differential regional blending or transition of environmental factors, the influence of locally controlling factors, and the adaptation of vegetation make difficult delineation of boundaries between regional and subregional areas; and, in some areas, there are inclusions of one area within another (e.g., "islands" within adjacent regions). Nevertheless, regional and subregional distinctions in vegetation are recognizable and mappable.

Physical, floral, and faunal regions of Texas were analyzed in detail by the U.S. Fish and Wildlife Service (1979). This reference is 30 years old, seldom cited, but important. It was prepared as a concept plan to determine unique wildlife ecosystems of Texas and contains detailed maps and extensive regional descriptions of flora and fauna with listings of many representative species. The wildlife section analyzes general zoography, distributional trends, and regional faunas with lists of species of special concern and threatened and endangered species.

CONCLUSIONS

The number of plant community types in Texas is dependent upon the classification system used (Bezanson 2000). However, an important result has been not only the identification of vegetation types; but, those that are both threatened and in need of protection. Thus, although boundaries of vegetational areas are difficult to assess, their plant communities are recognizable; thus, the concept of vegetational areas is especially beneficial in floral and faunal conservation and management. However, as proposed by MacRoberts and MacRoberts (2008), a new vegetational map of Texas based on total flora may provide additional helpful insights for establishing vegetational areas that better interpret the state's phytogeography.

ACKNOWLEDGMENTS

I am sincerely grateful to Michael H. MacRoberts (Louisiana State University, Shreveport), Stephan L. Hatch (Texas A&M University, College Station), and Barney L. Lipscomb (journal editor) who carefully reviewed the manuscript, corrected errors, and provided helpful comments and suggestions that greatly improved this paper.

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BOOK NOTICE

Sabeeha Merchant, Winslow R. Briggs, and Donald Ort (eds.). 2009. **Annual Review of Plant Biology, Volume 60.** (ISSN 1543-5008; ISBN 978-0-8243-0660-1, hbk.). Annual Reviews, 4139 El Camino Way, P.O. Box 10139, Palo Alto, California 94303-0139, U.S.A. (**Orders:** www.annualreviews.org, science@annualreviews.org, 800-523-8635, 650-493-4400). $89.00 indiv., 607 pp., cumulative indices, 7 1/2" × 9 3/8".

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VASCULAR PLANT SPECIES RICHNESS OF THE BIG THICKET, EAST TEXAS

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ABSTRACT

It has been claimed that the Big Thicket of southeastern Texas is exceptionally species rich when compared to other areas of North America. Extensive plant collecting in the Big Thicket has resulted in much more data than previously has been available. These data indicate that the Big Thicket is about average for species richness for comparable areas in the southeastern United States.

RESUMEN

Se ha dicho que el Big Thicket del sureste de Texas es excepcionalmente rico en especies comparado con otras áreas de Norte América. Recolecciones extensivas de plantas en el Big Thicket han aportado muchos más datos que los disponibles previamente. Estos datos indican que el Big Thicket tiene aproximadamente la media de riqueza de especies que áreas comparables del sureste de los Estados Unidos.

INTRODUCTION

For many years it has been claimed that the Big Thicket of southeastern Texas is exceptionally rich in plant species (see Cozine 2004; MacRoberts & MacRoberts 2004; Diggs et al. 2006 for reviews and literature). This claim has been difficult to test since until recently the Big Thicket region has been botanically understudied and underdocumented (MacRoberts et al. 2002; MacRoberts & MacRoberts 2007). However, this problem is now largely overcome by a floristic inventory of the major part of the Big Thicket National Preserve (MacRoberts et al. 2002; Brown et al. 2005, 2006a, 2006b, 2008a, 2008b, in prep a, b), a reexamination of earlier plant collections from the Big Thicket National Preserve (L.E. Brown pers. comm.), the recent publication of *Atlas of the Vascular Plants of Texas* (Turner et al. 2003) and *Illustrated Flora of East Texas* (Diggs et al. 2006), a floristic inventory of Walker, Polk, and San Jacinto counties (Nesom & Brown 1998), an inventory of a Polk County prairie (Brown et al. 2002), and an inventory of the Roy E. Larsen Sandylands Sanctuary in Hardin County (Matos & Rudolph 1985).

Using this information, we attempt to determine the species richness of the Big Thicket.

SETTING

It has long been realized that the Big Thicket is ill-defined and poorly delineated (McLeod 1971; Cozine 2004; Diggs et al. 2006). There are at least five delineations: 1) the "Broadest Conception" of the Big Thicket (Diggs et al. 2006), 2) the "Biological Survey" of Parks and Cory (1938), 3) the "Ecological Area" of McLeod (1971), 4) the "Traditional (Hunter's) Thicket" of the late nineteenth and early twentieth century (Diggs et al. 2006), and 5) the "Artificial Delineation" (Diggs et al. 2006) (see Diggs et al. 2006 and their figures 88 and 94 for details). We will be concerned only with the Broadest Conception ("Broadest Thicket" hereafter) and the Artificial Conception ("Artificial Thicket" hereafter) (Fig. 1), the reasons being that few pay attention to the Traditional Thicket and that the Artificial Thicket basically encompasses both the Biological Survey delineation and the Ecological Area delineation: the two delineations most frequently used.

The Broadest Thicket consists of part or all of 23 counties, a total of about 39,477 square km (Fig. 1) that includes the area between the cities of Nacogdoches and Liberty on a north-south axis and the Sabine River to the Brazos River on an east-west axis. The Artificial Thicket consists of seven and a half counties (Hardin, Jasper, Liberty [north half only], Montgomery, Newton, Polk, San Jacinto, and Tyler) and totals 17,974 square km (Fig. 1). It is located entirely within the Broadest Thicket area. The Broadest Thicket includes not only small isolated prairies, palmetto flats, oak floodplain, baygalls, wetland pine savanna, longleaf pine

Fig. 1. Location of Artificial Thicket and Broadest Thicket in the Big Thicket region of southeastern Texas.

upland, beech-magnolia forest, and xeric sandylands of the Artificial Thicket, but also coastal prairie on its southern edge, blackland prairie and post oak-hickory savanna on its western edge, and pine-oak-hickory forest to the north (Ajilvsgi 1979; Diggs et al. 2006 and references therein).

The Big Thicket National Preserve is located within the Artificial Thicket and consists of 14 units ranging from 2.2 square km to 100 square km and totaling 401 square km. Since the units were originally selected to provide a representative sample of community structure and flora (Peacock 1994; Diggs et al. 2006), a floristic inventory of the units should constitute a fair sample of the entire flora.

METHODS

Using the following sources (Matos & Rudolph 1985; Nesom & Brown 1998; MacRoberts et al. 2002; Brown et al. 2002, 2005, 2006a, 2006b, 2008a, 2008b, in prep. a, b; Turner et al. 2003; Diggs et al. 2006), we determined which species occurred in the Artificial Thicket and which occurred in the Broadest Thicket. Obviously, if a species occurred in the Artificial Thicket, it also occurred in the Broadest Thicket since the Artificial Thicket is encompassed entirely by the Broadest Thicket. If, however, a species only occurred in

Table 1. Number of Big Thicket plant species.

	Artificial Thicket	Broadest Thicket
Ferns & Gymnosperms	48	58
Monocots	573	748
Dicots	1144	1549
Total	1765	2355
Native species	1518	1937

the Broadest Thicket outside the Artificial Thicket, it was counted as occurring only in the Broadest Thicket. Only species were counted: if there were two or more varieties or subspecies, they were lumped.

RESULTS/DISCUSSION

Table 1 gives the number of ferns and gymnosperms, monocots, and dicots in the Artificial Thicket and Broadest Thicket. The total is 1765 species in the Artificial Thicket of which 1518 are native and 2355 species in the Broadest Thicket of which 1937 are native. Monocots account for 32.5 percent of the flora of the Artificial Thicket and 31.8 percent of the Broadest Thicket.

Diggs et al. (2006, see also Diggs et al. 2003), using earlier sources (up to about 2003), determined that the Artificial Thicket had 1826 species (native and naturalized) of which 31 percent were monocots. The figure 1826 is very close to ours and is between ours and the figure for the Broadest Thicket. The figure of 31 percent monocots is again almost identical to ours. The high incidence of monocots is indicative of the mesic to wet nature of the Big Thicket region of Texas (Diggs et al. 2006; MacRoberts & MacRoberts 2008). Dryer areas, such as North Central Texas, have fewer monocots (Diggs et al. 2006).

These figures are interesting because they are comparable to figures from other places at the same or approximately the same latitude in the southeastern United States. For example, the Florida Panhandle consists of 38,628 square km and has 2359 species, of which 31 percent are monocots, and 1989 are native (Clewell 1985). It is therefore almost identical in size, species number, and percent monocots to the Broadest Thicket. The Artificial Thicket is also comparable to other areas of equal size. For example, Bienville, Bossier, Caddo, Claiborne, Jackson, Lincoln, Ouachita, Union, and Webster parishes in northern Louisiana taken together consist of 16,601 square km and have approximately 1780 species, 30.1 percent of which are monocots (MacRoberts unpublished data developed from MacRoberts & MacRoberts 2006 and Thomas & Allen 1993–1998). However, the Florida Parishes of Louisiana (East Baton Rouge, East Feliciana, Livingston, West Feliciana, St. Helena, St. Tammany, Tangipahoa, and Washington), 200 km due east of the Big Thicket, consist of only 12,129 square km but have 1705 native species, of which 33 percent are monocots. If exotics are added, the total number probably would be between 2000 and 2100 species (MacRoberts unpublished data developed from Thomas & Allen 1993–1998).

These findings support our previous analysis of species/area across the south, in which we used the Diggs et al. (2006) figure of 1826 species, and found that the Big Thicket was not exceptional in species numbers but is about average for the southeastern United States (MacRoberts et al. 2007).Thus, our current analysis confirms our previous conclusion. Although the data are not available, it may transpire that the Big Thicket is slightly below average for similar sized areas at the same latitude in the southeastern United States. The data for the Florida Parishes of Louisiana suggest this, but until other areas such as southern Mississippi, Alabama, Georgia, and northern Florida are sampled, no conclusion is possible.

While we are in process of redefining the Big Thicket, it should be remembered that the Big Thicket is important to preserve because hundreds of southeastern species reach their range limit in the Big Thicket. The Big Thicket is, therefore, a boundary area and is important for a variety of reasons: boundary plants are often genetically unique and peripheral populations are often more sensitive to environmental change and can act as ecological indicators (Diggs et al. 2006). But, the most important reason for considering the

Big Thicket immensely valuable was made by Donovan Correll years ago before the Big Thicket became a preserve. Testifying before the Senate committee in Beaumont in 1970, he pointed out that the vast pine hardwood forest that characterized the southeastern United States had no areas that were preserved. He said: "We ought to have a representation of the great Southeastern pine hardwood forests somewhere, and since the development is so optimum here in Texas," then the Big Thicket would be ideal for that representation.

ACKNOWLEDGMENTS

Larry Brown provided many useful comments on an earlier version of this paper including his personal observations on species richness on the southeastern United States. George Diggs and an anonymous reviewer had a number of valuable comments about the manuscript.

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BOOK NOTICE

Hu Ren-liang, Wang You-fang, and Marshall R. Crosby (eds.-in-chief), with Si He (ed.). 2007. **Moss Flora of China, Vol. 7. English Version. Amblystegiaceae – Plagiotheciaceae.** (ISBN Vol. 7: 978-1-930723-77-1, hbk.). Science Press (Beijing) and Missouri Botanical Garden Press (St. Louis), 4344 Shaw Boulevard, St. Louis, Missouri 63110-2291, U.S.A. (**Orders:** www.mbgpress.org, mbgpress@mobot.org, 314-577-9534, 314-577-9594 fax). $85.00, 258 pp., 8 5/8" × 11 1/4".

From the Introduction: "The *Moss Flora of China*, English Version, is a series of eight volumes dealing with all mosses known to be native or naturalized in China. It contains descriptions, identification keys, illustrations of Chinese endemic and East Asian taxa, habitat information, distributional ranges outside of China, specimen citations, and distribution maps of all accepted taxa. The present volume is the seventh to be published in the series. It treats 41 genera and 188 specific and infraspecific taxa, including two new combinations... The last volume of the series, Volume 5, treating such large families as Orthotrichaceae, Leucodontaceae, Pterobryaceae, Meteoriaceae, and Neckeraceae will be completed by the end of 2009."

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A CLASSIFICATION OF GEOGRAPHIC ELEMENTS AND ANALYSIS OF THE FLORA OF BIG BEND REGION OF TEXAS

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ABSTRACT

The flora of the Big Bend region in the Trans-Pecos Vegetational Area of SW Texas was studied from a biogeographical perspective. A checklist of the designated flora was extracted primarily from the *Synthesis of the North American Flora* and data concerning the general distribution of species were obtained from the literature, the "*Synthesis*," and other on-line databases. There are 1587 native species in 592 genera and 125 families in the flora. These species, based on their contemporary distribution outlines, were classified into 19 geographic (floristic) elements. The genera were classified into 19 geographic groups based on their general distribution. Herein is presented a classification scheme of geographic elements (geoelements), the checklist accompanied by the geoelement descriptions, and the analysis of the flora. The Big Bend region flora—being on the boundary of two subkingdoms, the Madrean and Boreal—has a complex pattern of connections, with predominance of the autochthonous xerophytic taxa evolved from the Madro-Tertiary geoflora stalk. Laurasin (Arcto-Tertiary) flora derivatives play a lesser role. The strongest connections of the flora are with Mesoamerica-South America. The Madrean species (66%) and especially the Chihuahuan endemics (26%) are most numerous. In the generic composition, south-western and western North American, followed by tropic/subtropical, genera are much better represented than north and eastern American temperate genera. Eastern and western Northern Hemisphere's connections across the Atlantic, show three different patterns: northern early Tertiary migrations of the Laurasian mesophyllous genera, diversification of older Madro-Tethyan subtropical genera along the Tethys seaway, and migration westward along the southern Tethys shore of termophyllous ancient taxa originated or preserved in the Horn of Africa region.

RESUMEN

La flora de la región de Big Bend en el área de vegetación de Trans-Pecos en el de SW Texas se estudió desde la perspectiva biogeográfica. Primeramente se extrajo un catálogo de la flora de la *Synthesis of the North American Flora* y se sacaron datos bibliográficos relativos a la distribución general de las especies, la "*Synthesis*," y otras bases de datos on-line. Hay 1587 especies nativas en 592 géneros y 125 familias en la flora. Estas especies, según sus perfiles de distribución contemporánea, se clasificaron en 19 elementos geográficos (florísticos). Los géneros se clasificaron en 19 grupos geográficos según su distribución general. Aquí se presenta un esquema de clasificación de elementos geográficos (geoelementos), el catálogo acompañado por las descripciones de los geoelementos, y el análisis de la flora. La flora de la region Big Bend—en la frontera de dos subreinos, el Madreano y el Boreal—tiene un patrón complejo de conexiones, con predominio de taxa xerofíticos autóctonos evolucionados del núcleo florístico Madro-Terciario. Las derivaciones de la flora Laurasina (Arcto-Terciaria) tienen un papel menor. Las conexiones más fuertes de la flora son con Mesoamérica-Sur América. Las especies Madreanas (66%) y especialmente los endemismos Chihuahuanos (26%) son los más numerosos. En la composición genérica, los géneros del suroeste y oeste norteamericano, seguidos por los tropicales/subtropicales, están mucho mejor representados que los templados del norte y este americano. Las conexiones este-oeste del hemisferio norte a través del Atlántico, muestran tres patrones diferentes: migraciones al norte en el Terciario temprano de géneros Laurasianos mesófilos, diversificación de los géneros subtropicales más viejos Madro-Tetianos a lo largo de de la ruta del Tetis, y migración hacia el oeste a lo largo de la costa sur del Tetis de los taxa viejos termófilos originados o preservados en la región del cuerno de in África.

INTRODUCTION

The Trans-Pecos region of Texas or West Texas Vegetational Area (Correll & Johnston 1970) is distinct from that of surrounding areas in Texas because of its numerous mountain systems and low arid basins with elevation ranges from 305 to 2388 m (1000–7835 ft) (Powell 1998). It lies on the northern edge of the Chihuahuan Subprovince of the Sonoran Province of Takhtajan's floristic system (Takhtajan 1986) and thus on the boundary of two Subkingdoms of the Holarctic Kingdom: the Boreal and Madrean. An analysis of such flora can provide a good opportunity to reveal proportions of different floristic elements, to look for Arcto-Tertiary and Madro-Tertiary (Axelrod 1958; Raven & Axelrod 1987) relicts, and to specify the

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level and areas of endemism (Platnick 1991; Morrone & Crisci 1995). Northern and eastern limits of the Madrean region are difficult to delineate and they were subject of debate in the North American literature (Good 1974; Cronquist 1982; Morrone et al. 1999; McLaughlin 2007; see McLaughlin 2007:31 for comparison; also Katinas et al. 2004; and Fenstermacher et al. 2008). The Northern Madrean boundary is a composite area were different distribution tracks overlap and partial floras of different types of vegetation in the mountains represent historical elements of different origins, affinities, and age, both relictual and progressive, autochthonous, and migrational.

The flora of three counties in the Big Bend region—Brewster, Presidio, and Jeff Davis—was chosen to test the floristics in the Chihuahuan Subprovince. A major objective is to reveal the taxonomic proportions and biogeographic affinities of the plant taxa in the region.

MATERIALS AND METHODS

Using primarily the *Synthesis of the North American Flora* (Kartesz & Meacham 2002; Kartesz 2008), a checklist of the flora of Brewster, Presidio, and Jeff Davis counties in Trans-Pecos was compiled. The non-native species were excluded. Several new species were added to the checklist draft after it was compared with the one of the Dead Horse Mountains, Big Bend National Park (Fenstermacher et al. 2008). Taxonomic counts of the families, genera, and species were performed. The distributional and other data were obtained from the Synthesis of the North American Flora (Kartesz & Meacham 2002), Tropicos (Tropicos.org.), Flora of North America, Digital Flora of Texas databases, the Onagraceae website (Wagner & Hoch 2005), the literature (Correll & Johnston 1970; Powell 1998; Turner et al. 2003; Diggs et al. 1999; Villarreal 2001), and other sources. The distribution outlines of all the species in the flora were studied. Congruent distributions of two or more species were named after well known chorionomic units (Takhtajan 1986; Thorne 1993; Rzedowski 1978) or in geographic terms. Each species was thus referred to and treated as a particular geographic element, or geoelement (Saghatelyan 1997a, b) of the flora. All the species were classified into 19 geoelements according to their general distributional patterns revealed during the current study. The distribution data on the genera were retrieved from Wielgorskaya (1995) and Mabberley (1997). The genera were classified into 19 groups based on their distribution outlines.

The species list (Appendix 1) for the above-mentioned counties was prepared with the major objective of defining the geoelements individually and collectively represented. Proportions of geoelements in a flora are robust characteristics which are not sensitive to minor nomenclatural changes. "Good species" always have "good ranges" and they usually serve as a basis of biogeographic analysis. The ranges of some species could not be referred to a particular geoelement; they are noted with a question mark in the checklist and are omitted from the analysis. Major outcomes expected from the analysis are:

1. Proportion of the species and genera of the Boreal and Madrean Subkingdoms and their provinces and subprovinces in the flora.
2. Northern temperate versus southern subtropic & tropical connections of the flora.
3. Proportion of the species confined to one, two, or more subprovinces of the Sonoran Province.
4. The weight of the northern Madrean species in the Madrean element of the flora.
5. Connections of the Madrean and Tethyan subkingdoms.
6. Major migrational tracks.

RESULTS

A CLASSIFICATION SYSTEM OF GEOGRAPHIC ELEMENTS AND THEIR PROPORTIONS IN THE BIG BEND REGION FLORA (TABLE 1)

Abbreviations: C–center; **TX**–Texas; **CA**–California; **CO**–Colorado; **AZ**–Arizona; **OK**–Oklahoma; **MO**–Missouri; **WO**–Wyoming; **SMO**–Sierra Madre Oriental; **Rocky M**–Rocky Mountains Province; **Mont**–montane; **US**–United States; **Mesoam**–Mesoamerican; **Gulf Coast**–Atlantic and Gulf Coastal Plain Province; **Tr–Pecos**–Trans-Pecos; **J Davis**–Jeff Davis; **c**–county; **cc**–counties; **Warm**–warm temperate.

TABLE 1. Proportions of geographic elements in the Big Bend flora.

Geoelement	Subelement	Number of species
Madrean		192
Sonoran-Chihuahuan		80
Sonoran		82
Chihuahuan		253
Chihuahuan-Tamaulipan		50
SW North American		149
	S Rocky Mountain-Madrean	20
	SWC US & SWC N American	64
	Apachian/SW US & SW N American	65
W US/W N American		133
	WUS/W N American	76
	WC US/WC N American	29
	S Great Basin-Sonoran/Chihuahuan	9
	Amphitropical	19
S TX Endemic		101
Prairie		88
EN American		37
Comanchian/SC US		45
N American		98
Mesoamerican		84
American		101
	American wide	96
	Western American	5
Tropical/Subtropical		32
	American-African	6
	Tropical/Subtropical	26
Holarctical		21
Polichorous		14
Not established		25
Total		1587

1. **Polichorous:** wide distribution on several continents. There are 14 species (sp.) of herbaceous wetland (*Veronica peregrina*), aquatic (*Potamogeton nodosus*), and weedy (*Plantago major*) plants of this geoelement in the flora.
2. **Holarctical:** wide ranges in north temperate latitudes of the New and Old World; 21 mesophytic species. Among them are 6 sp. of grasses (*Bromus ciliatus*), 2 sp. of horsetails (*Equisetum hyemale*), and a fern (*Asplenium trichomanes*). Other large north temperate genera have just 1–2 sp. each (*Campanula rotundifolia, Ranunculus sceleratus,* and *Artemisia campestris*) in the flora.
3. **Trop/Subtr:** wide distribution in tropical and subtropical latitudes; 32 species. Mesophytic, aquatic and wetland species, especially of herbaceous habit (*Thypha domingensis, Bacopa monieri*) predominate in this group. There are also several shrubs (*Sapindus saponaria, Parkinsonia aculeata,* and *Acacia farnesiana*) of pantropical or subtropical distribution. Two sub-elements of Trop/Subtr element are listed below.
    - **3a. American-African:** the previous type restricted to America and Africa. Seven species: three of grasses (*Echinochloa crus-pavonis*), three of sedges (*Cyperus squarrosus*), and one fern (*Cheilanthes bonariensis*).
    - **3b. Warm Temperate/Subtropical:** mostly in subtropical and warm temperate regions. Only 11 sp. of grasses (*Digitaria sanguinalis*) are in this group.
4. **American:** wide distribution in the Americas; 101 sp. Here are mostly subtropical weedy grasses (29 sp.: *Bouteloa barbata*) and sedges (8 sp.: *Cyperus seslerioides*), as well as temperate Asteraceae (6 sp.: *Conyza*

canadensis). Western American (Cordilleran) genera have six species (*Muhlenbergia rigida, Epilobiium ciliatum*), while 5 species of *Amaranthus* and *Heliotropium* are mostly Caribbean.

4a. American Trop/Subtr: widely distributed in tropical and subtropical (warm temperate) parts of the Americas. This sub-element has 30 of the 101 sp. of the American element with the grasses (*Cenchrus myosuroides*) being especially numerous. Other examples are *Tillandsia recurvata, Solanum elaeagnifolium, Phyla nodiflora,* and *Ipomoea cardiophylla*.

5. North American: more or less wide ranges in temperate regions of North America; 98 mesophytic species. They either belong to widely north temperate genera (*Maianthemum racemosum, Carex hystericina,* and *Vicia americana*), north American genera (*Solidago gigantea, Lobelia cardinalis, Monarda fistulosa*), or cosmopolitan genera with large sections in temperate latitudes (*Euphorbia cyatophora*). Herbaceous habit, especially in the grasses (18 sp.), sedges (8 sp.), Asteraceae, and Euphorbiaceae (6 sp. each) predominate. A few older montane woody species have interesting ranges: either absent in the south-eastern and south-central region (*Prunus virginiana*), poorly represented in the western and absent in the central (*Cephalanthus occidentalis*) region, or those that tend to the Rocky Mountain (*Cheilanthes feei*) Region.

6. East North American: wide ranges in the Atlantic North American Region of Cronquist (1982). Representatives of ancient Laurasian genera are essential among the 37 sp. of this geoelement (*Ostrya virginiana, Carya ilinoensis,* and *Clematis pitcheri*). A few species however have tropical connections (*Cocculus carolinus, Celastrus scandex,* and *Nothoscordum bivalve*).

6a. Gulf Coast-(Caribbean): with ranges in the namesake provinces (*Thelipteris ovata, Melothria pendula*).

6b. Appalachian: with ranges in the namesake province (*Ostrya virginiana, Melica nitens*).

7. Comanchian/ SC US: Edwards Plateau westward to the Trans-Pecos extending northward into central Oklahoma or further to Ozark Plateau, southward into northeastern Mexico and western Lousiana, mainly in the limits of the Comanchian Subprovince of McLaughlin (2007). There are 46 species in this geoelement like *Juniperus ashei, Lupinus texensis,* and *Scutellaria wrightii*, with some having disjunct relictual ranges (*Leptopus phyllanthoides*).

8. Prairie: wide ranges in the North American Prairies Province of Cronquist (1982); 85 mostly herbaceous species. Biggest group of 24 sp. is in Asteraceae (*Liatris punctata, Hymenopappus scabiosaceous*), especially in the Heliantheae s.l. (Panero & Funk 2002). Poaceae (*Bouteloua dactyloides, Schedonnardus paniculatus*), and papilionaceous Fabaceae (*Astragalus lotiflorus, Dalea aurea*) have 7 sp. each. Remaining species are in large temperate genera (*Oenothera triloba, Salvia azurea*) with big centers of diversity in western America and Mexico.

8a. S Prairie/SC North American: from Central and South Texas extending northward to adjacent states and southward to northern Mexican Plateau (*Eryngium leavenworthii, Argythamnia humilis, Rhus lanceolata,* and *Gaillardia suavis*).

9. W North American: wide ranges in the entire western North America or its parts mostly north of Mexico. Among the 133 sp. of this geoelement 28 sp. of Asteraceae (*Brickelia californica, Erigeron divergens*) prevail, followed by 18 sp. of Poaceae (*Agrostis exarata*) and 9 sp. of Brassicaceae (*Stanleya pinnata*). Western American genera have numerous species (*Glossopetalon spinescens, Cryptantha cinerea*) including the dominants in different types of communities. Examples range from those of montane forests (*Pinus ponderosa, Quercus gambelii,* and *Cercocarpus montanus*), Rocky Mountain and Madrean woodlands and shrublands (*Juniperus scopulorum, Rhus trilobata, Holodiscus dumosus*), to widely distributed xerophytic (*Opuntia polyacantha*) as well as riparian (*Salix exigua*) species.

9a. WC US/ WC North American: includes western mountainous (not Pacific) region and western half of the Prairies Province in the United States/or southward to central Mexico; this element supports S. McLaughlin's (2007) Western Region. Of the 133 sp. of W North American element, 29 sp. are in this sub-element. They belong to large temperate genera (*Astragalus, Cirsium,* and *Lithospermum*), North American genera (*Monarda pectinata, Oenothera albicaulis*), or a few tropical (*Heliotropium convolvulaceum*) genera.

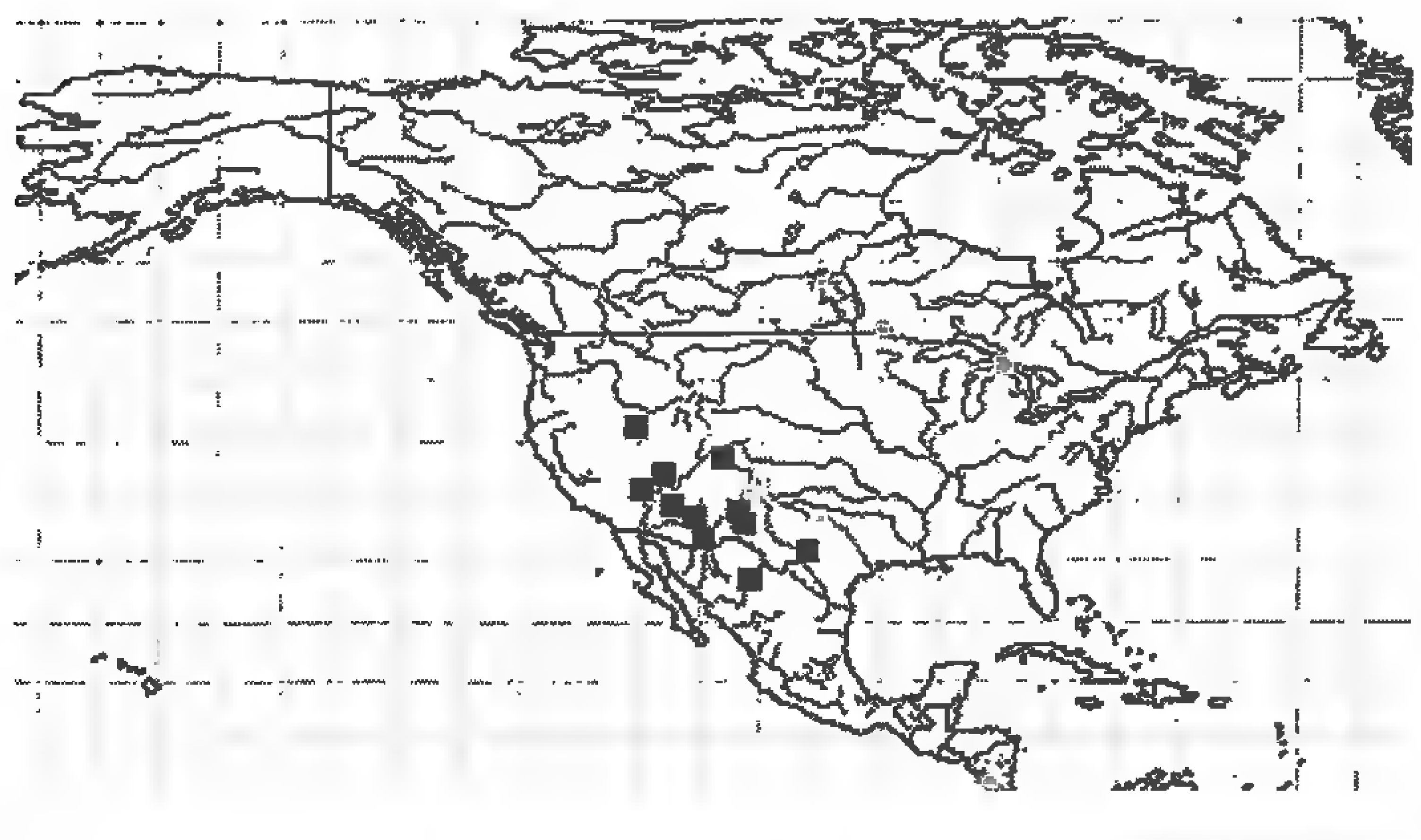

Fig. 1. Distribution of *Yucca baccata*. SW N American element. Source: Tropicos.org. Missouri Botanical Garden. 27 Mar 2009 <http://www.tropicos.org>.

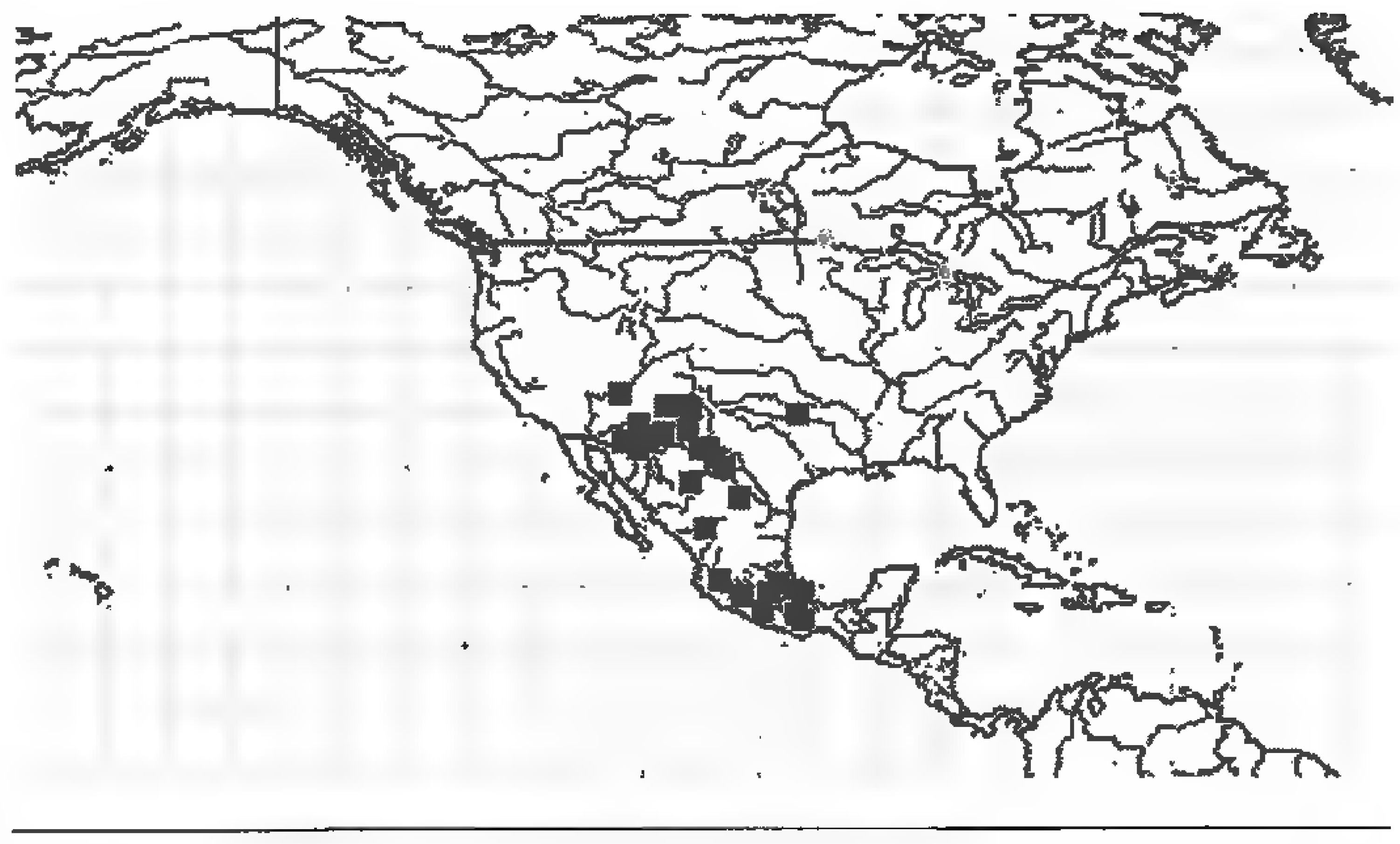

Fig. 2. Distribution of *Juniperus deppeana*. Madrean element. Source: Tropicos.org. Missouri Botanical Garden. 27 Mar 2009 <http://www.tropicos.org>.

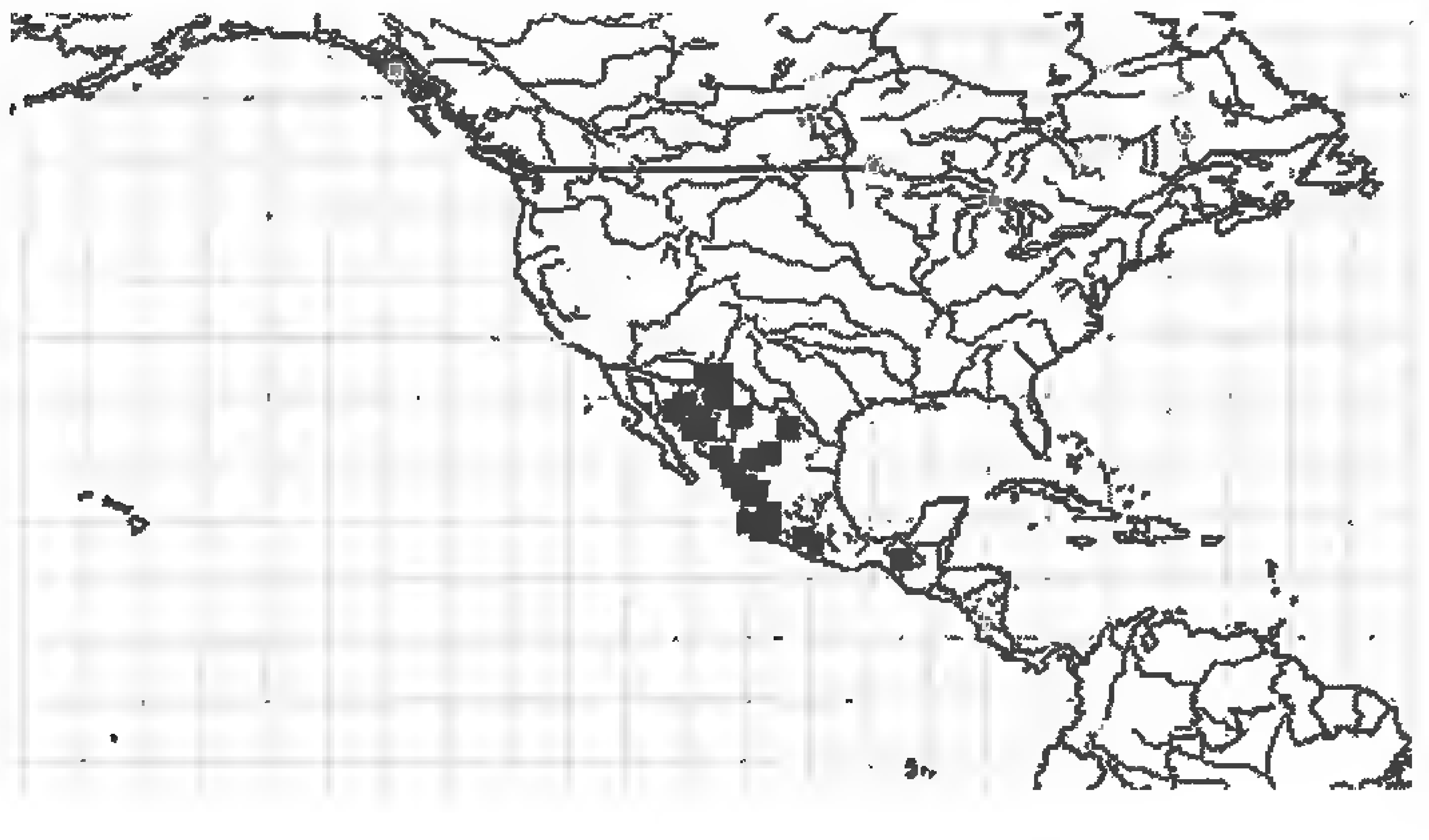

Fig. 3. Distribution of *Kallstroemia grandiflora*. Madrean (W) element. Source: Tropicos.org. Missouri Botanical Garden. 27 Mar 2009 <http://www.tropicos.org>.

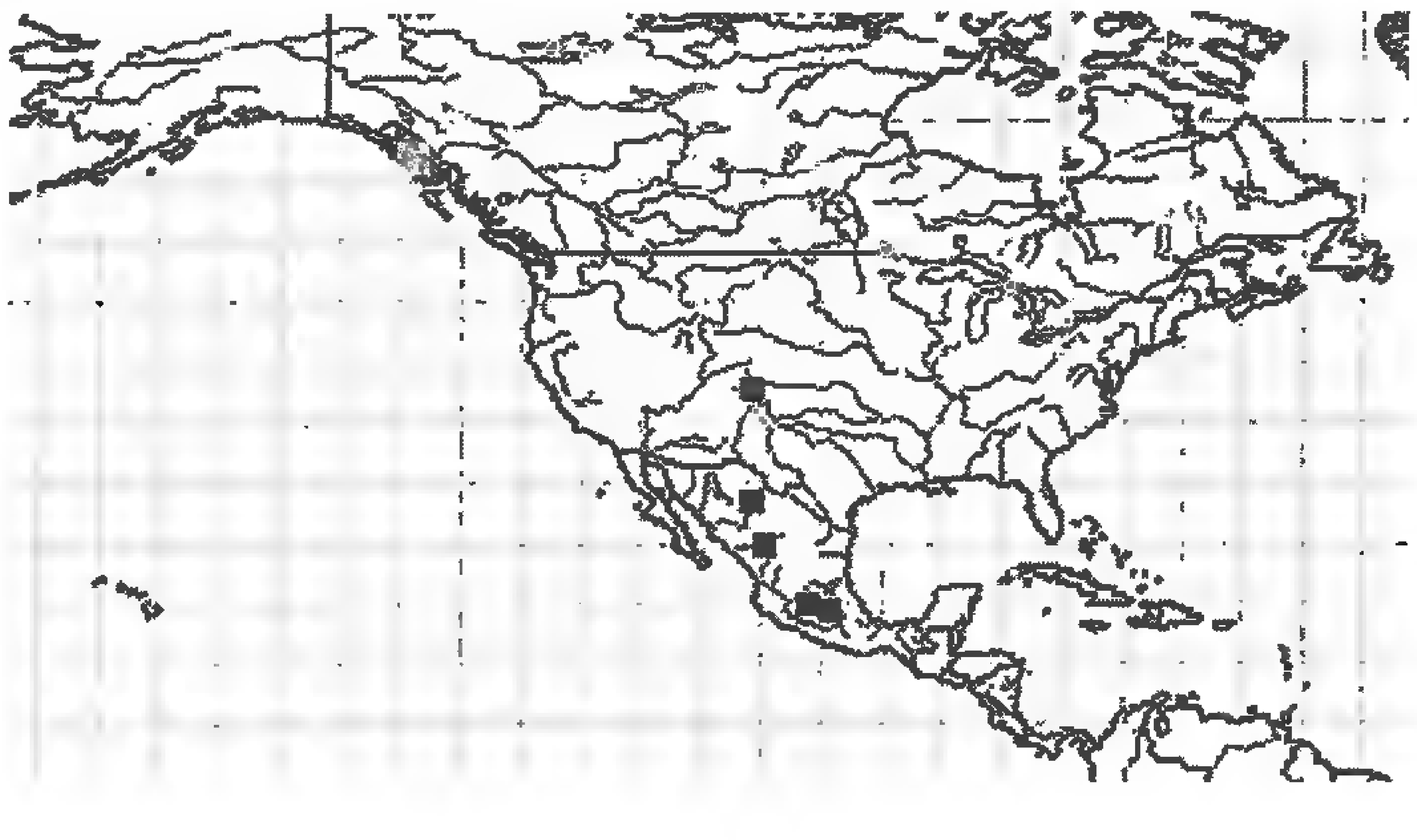

Fig 4. Distribution of *Cleome multicaulis*. South Rocky Mountain-Madrean element. Source: Tropicos.org. Missouri Botanical Garden. 27 Mar 2009 <http://www.tropicos.org>.

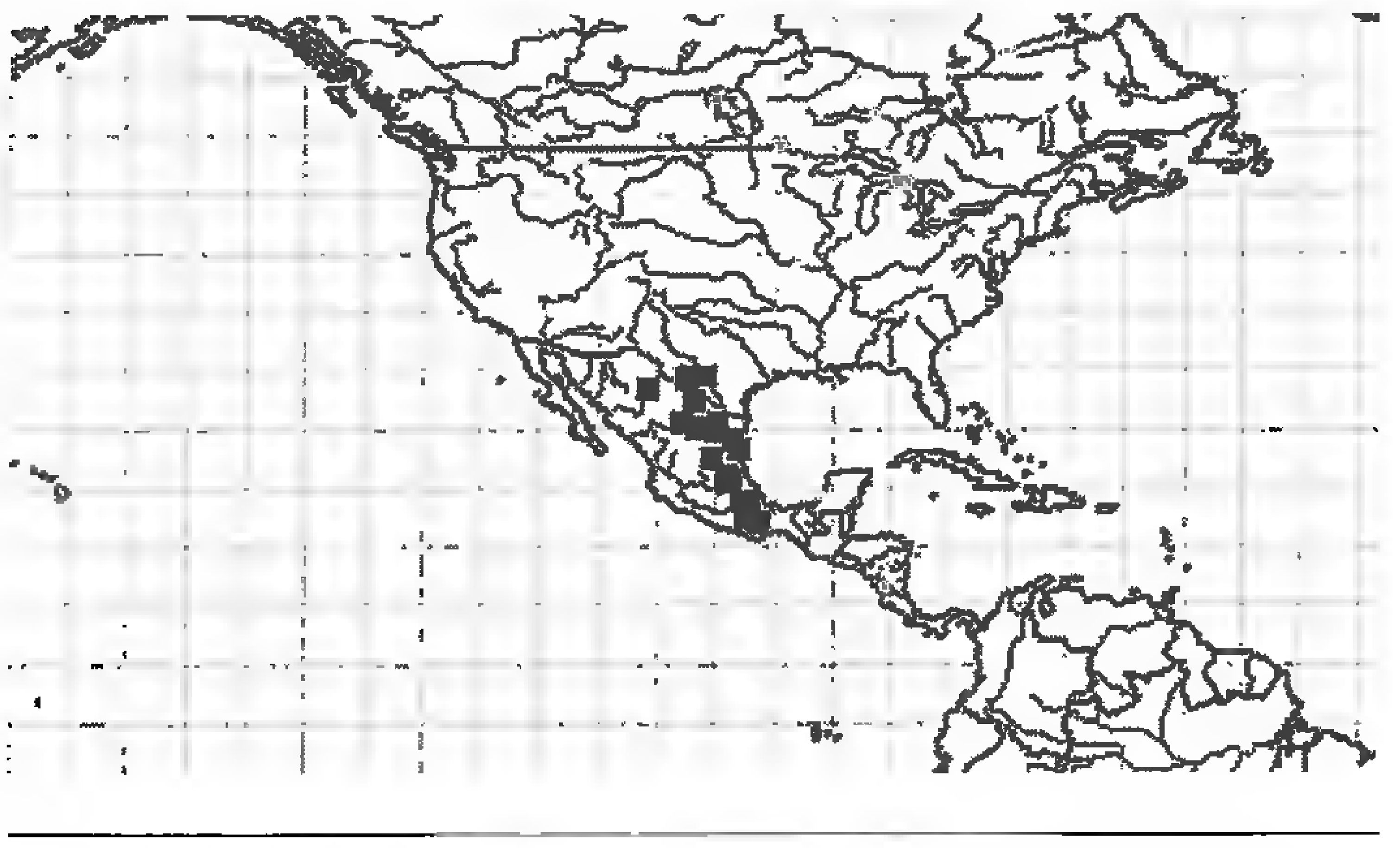

Fig. 5. Distribution of *Rhus virens*. E Madrean element. Source: Tropicos.org. Missouri Botanical Garden. 27 Mar 2009 <http://www.tropicos.org>.

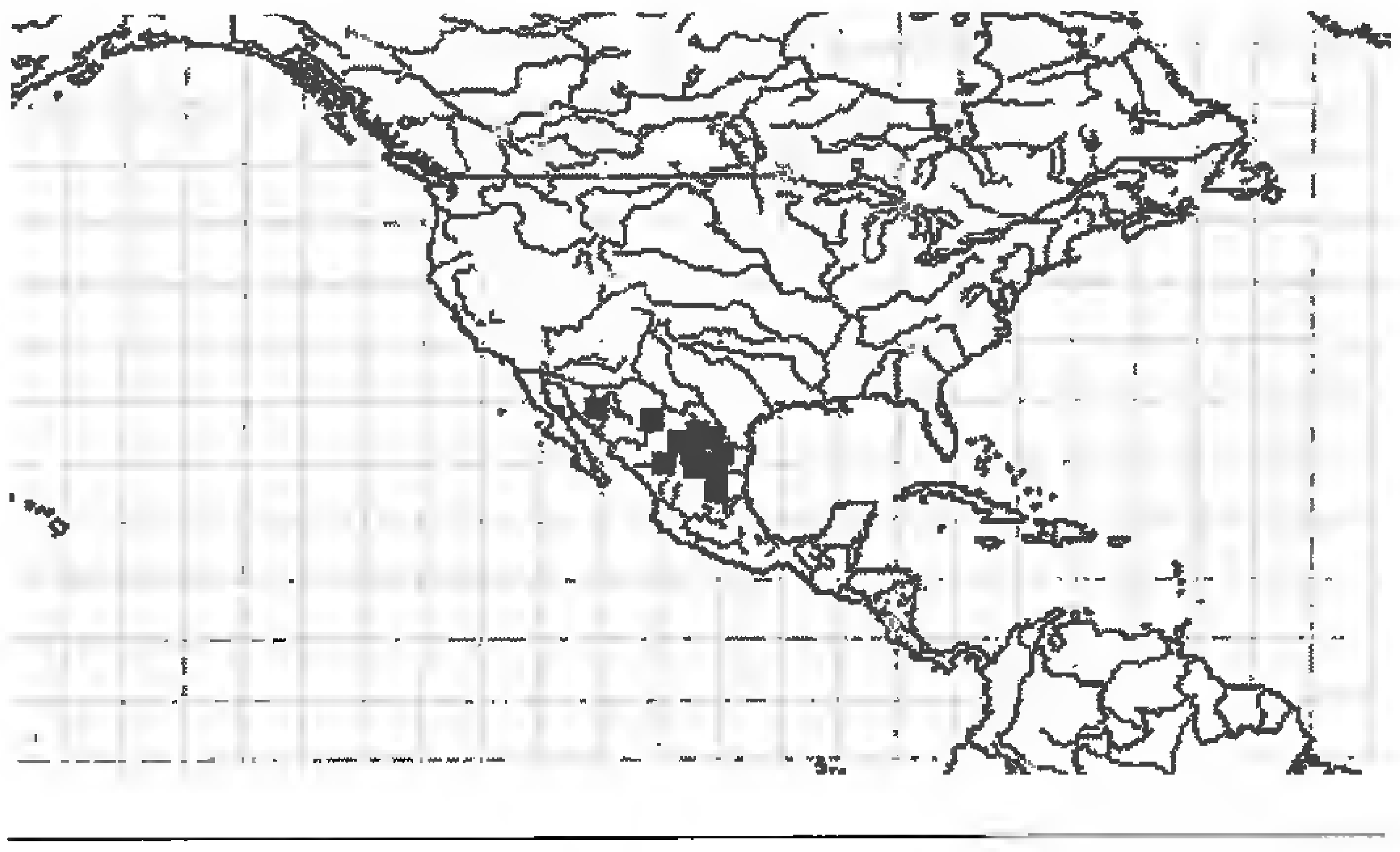

Fig. 6. Distribution of *Peganum mexicanum*. Sonoran-Chihuahuan element. Source: Tropicos.org. Missouri Botanical Garden. 27 Mar 2009 <http://www.tropicos.org>.

10. SWC North American/ SWC US: more southern/eastern than the previous geoelement: from Colorado Plateau, southern Rocky Mountains and south-western part of the Prairies Province southward to the US border or Sierra Madre Occidental/more eastern central Mexico. Among 64 species of this element those of western and south-western North American genera predominate. The grasses (11 sp.), Asteraceae (9 sp.), and Fabaceae (5 sp.) are followed by species of typical American desert genera in Agavaceae (*Nolina texana*), Hydrophyllaceae, Onagraceae, Cactaceae, etc. Several species of this element are of woody habit (*Quercus mohriana, Lonicera albiflora*).

11. SW North American/ SW US: southern part of the Rocky Mountain Province, Colorado Plateau, southern and eastern Great Basin, southeastern California (not always), both Mohavean and northern Sonoran Subprovinces of the Cronquist's (1982) system eastward through New Mexico to southwestern Texas and southward to adjacent northern Mexico. A group of 65 xerophytic species including 5 out 7 species of Hydrangeaceae of the Big Bend flora, *Ephedra torreana, Yucca baccata* (Fig. 1), *Opuntia phaeacantha* and other desert dominants. All herbaceous species are those of desert genera (*Mentzelia multiflora, Hackelia pinetorum,* 9 sp. each of Poaceae and Asteraceae, etc.). There are two subtypes:

11a. Apachian: from central to southeastern Arizona, western New Mexico, to northeastern Sonora, and northwestern Chihuahua as delineated by McLaughlin (2007). Among species of the southwestern element 20 sp. are in this sub-element (*Penstemon jamesii, Boerhavia torreyana,* and *Phlox nana*).

11b. S Great Basin-Sonoran-Chihuahuan: ranges from the southern half of the Great Basin Province southward into Sonoran and Chihuahuan Subprovinces of Cronquist (1982). Nine species are restricted to this area, mostly those of south-western genera (*Pennellia longiflora, Abronia angustifolia*).

12. Amphitropical: disjunctive ranges in warm temperate deserts of the western North and South America; 20 species. Among them are 6 sp. of grasses, 3 sp. each of Fabaceae and Asteraceae and one in each of other desert genera (*Aloysia gratissima, Kallstroemia parviflora,* and *Mentzelia albescens.*)

13. Madrean wide: ranges embracing Takhtajan's (1987) Madrean Region in some cases excluding the California Province (Figs. 2, 3). Most spectacular group of 192 species with the highest number of woody species-dominants in various types of mountain and desert communities. The prevailing families are: Asteraceae (30 sp.), Poaceae (24 sp.), Fabaceae (15 sp.), Euphorbiaceae (15 sp.), and Pteridaceae (11 sp.). Very important are 4 sp. each of Cupressaceae, Rhamnaceae and Oleaceae, 3 sp. of Zygophyllaceae, including *Larrea tridentata,* 2 species of *Ephedra, Juglans major, Garrya ovata, Rhus virens* and *Morus microphylla.* About 30 species of the flora with wide Madrean distribution are absent in California and most of the Great Basin Provinces. The madrean element has following subelements.

13a. S Rocky Mountain-Madrean: along the Rocky Mountains from Colorado Plateau southward to Sierra Madre Occidental Province or further into the Madrean mountains (Fig. 4). There are 20 species in this sub-element mostly of Asteraceae (5 sp.), Brassicaceae (3 sp.), and Malvaceae (3 sp.). The species of western American genera (*Castilleja integra*) predominate, however a few species are of tropical/warm temperate genera (*Cleome multicaulis*).

13b. East Madrean: mostly in the Sierra Madre Oriental Province of Morrone et al. (1999) extending northward to the Edwards Plateau and mountains in Trans-Pecos (Brewster, Jeff Davis, and Presidio counties). The following species highlight this sub-element: *Rhus virens* (Fig. 5), *Fraxinus cuspidata, F. greggii, Croton incanus, Euphorbia bifurcata, Dalea gerggii, D. frutescens, Centaurium calycosum, Oenothera calcicola, O. primiveris,* and 6 sp. of Pteridaceae.

13c. North Madrean: ranges in northern, mostly US part of the Madrean Region of Takhtajan (1987), southward to Mexican part of the Sonoran Subprovince and south-western Texas. This sub-element has 57 sp. of the madrean element in the genera with following ranges: south-western North American (*Wislizenia refracta*), central-to tropical American (*Matelea parviflora*), mostly N American (*Symphoricarpos palmerii*), western N and S American (*Hedeoma nana*), and tropical/subtropical American (*Proboscidea parviflora, Boerhavia wrightii*). Several species are in cosmopolitan (*Chamaesyce,* 5 sp.) and north temperate (*Eriogonum,* 3 sp., *Galium*) genera.

14. Mesoamerican: wide ranges in Mesoamerica and Caribbean Region extending to southern United States and northern South America; 83 species. Most of them are among the Asteraceae (17 sp.), grasses (9 sp.), legumes (8 sp.), and ferns (5 sp.). The species of Mesoamerican-Madrean (*Bouvardia ternifolia*), Mesoamerican-S American (*Margaranthus solanaceus*), tropical (*Cyclanthera dissecta*) and subtropical American (*Macroptilium gibbosifolium*), as well as widely American (*Oenothera hexandra*) genera prevail. Two species, *Arbutus xalapensis* and *Helianthemum glomeratum,* are in the Madro-Tethyan genera.

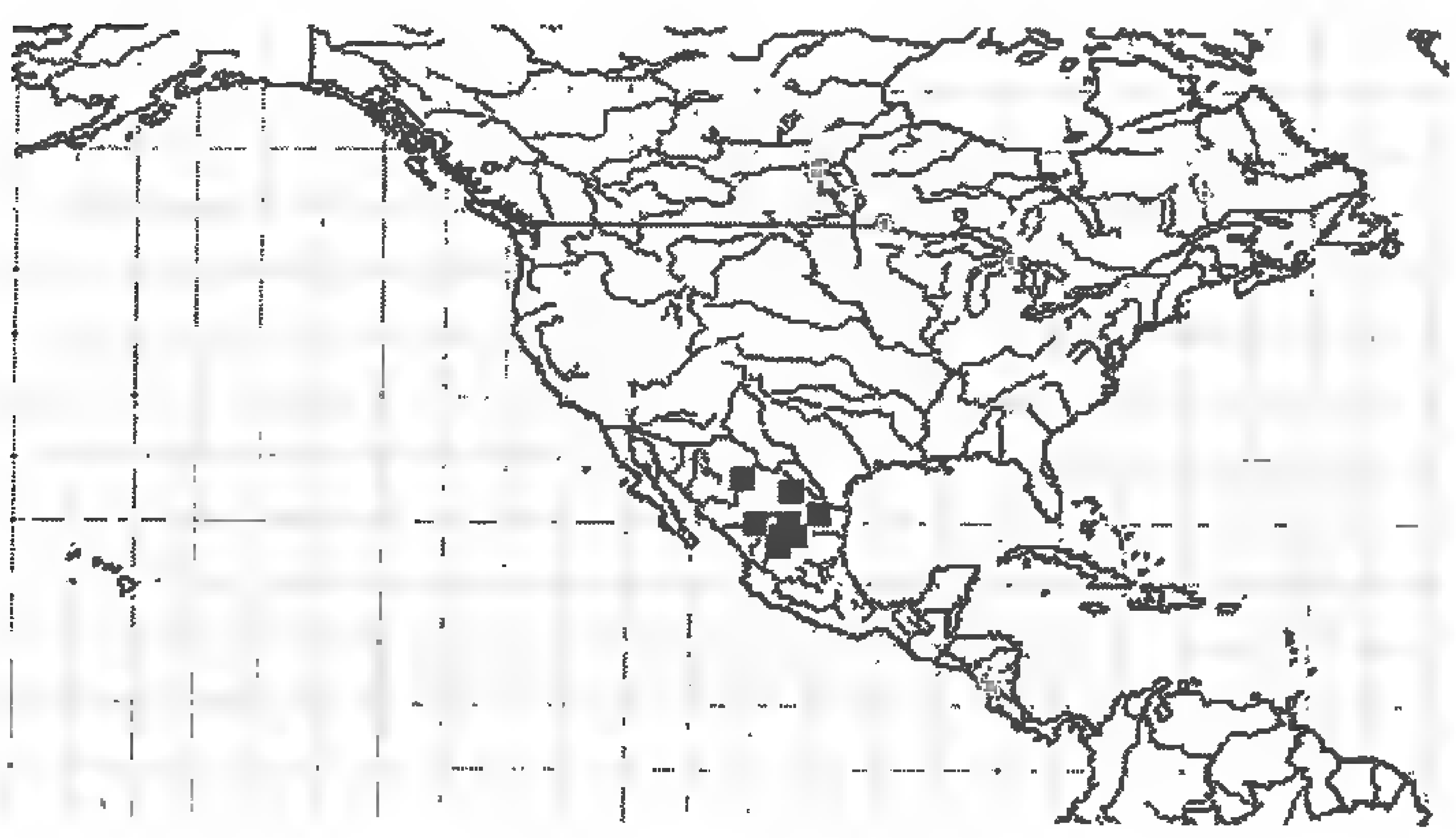

Fig. 7. Distribution of *Condalia ericoides*. Chihuahuan element. Source: Tropicos.org. Missouri Botanical Garden. 27 Mar 2009 <http://www.tropicos.org>.

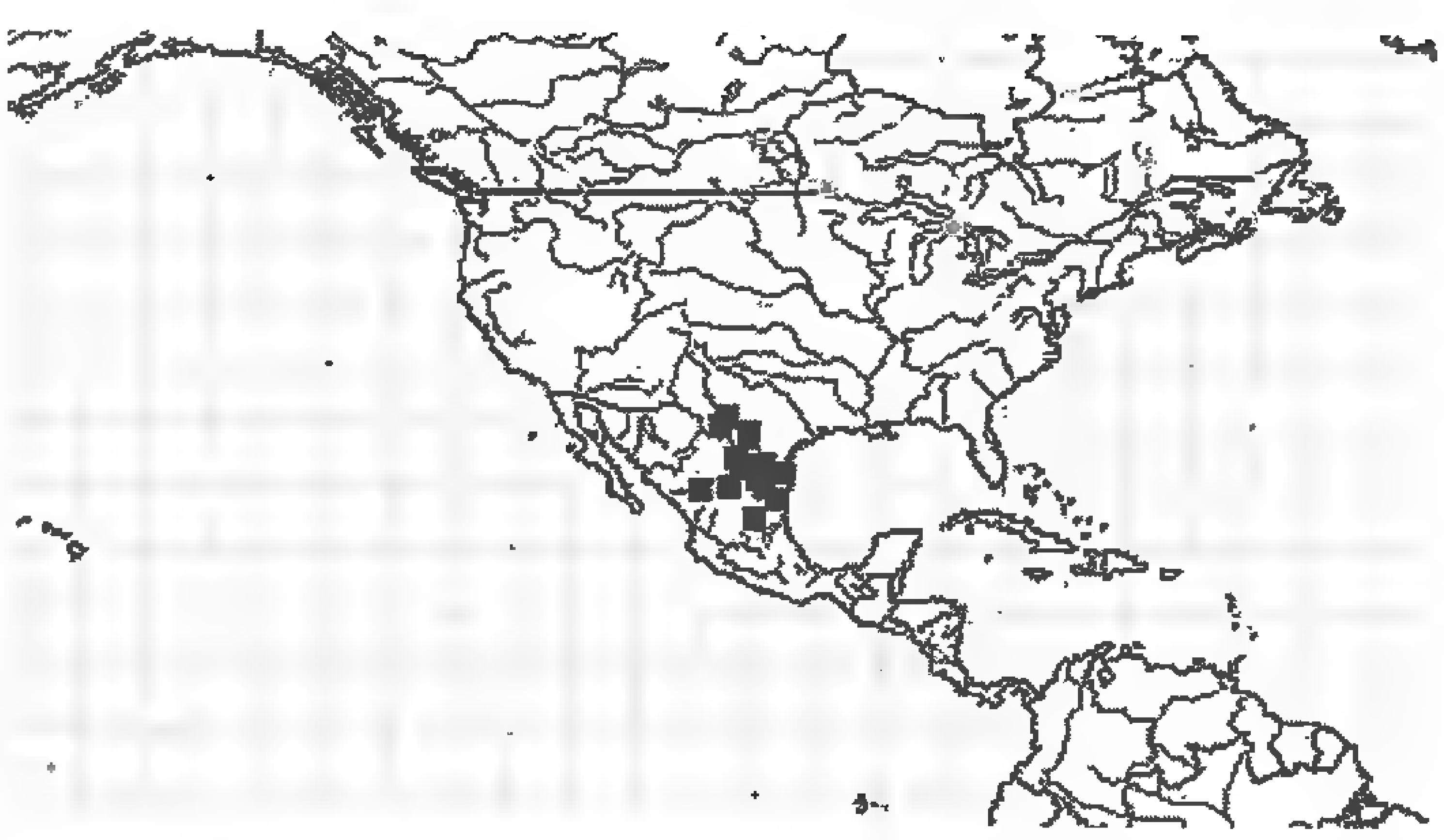

Fig. 8. Distribution of *Leucophyllum frutescence* Chihuahuan-Tamaulipan element. Source: Tropicos.org. Missouri Botanical Garden. 27 Mar 2009 <http://www.tropicos.org>.

14a. Mesoamerican-Madrean: wide ranges in the Madrean Region and Mesoamerica southward to Costa Rica. Of the Mesoamerican element, 19 sp. are in this subelement (*Quercus rugosa, Chamaesyce villifera,* and *Desmodium psilophyllum*).

15. Sonoran wide (or Sonoran Province): embracing all subprovinces of the Sonoran Province of Cronquist (1982); 82 xerophytic species including many dominants of the sonoran desert communities. The legumes (8 sp.: *Calliandra humilis*), Malvaceae, and Nyctaginaceae (6 sp. each) prevail among them. Especially characteristic are those of western American (*Aloysia wrightii, Garrya wrightii*) and SW N American (*Chilopsis linearis*) genera, and some of more widely American genera (*Verbena perennis*). Also very important are four species each of Cactaceae (*Opuntia*) and Rhamnaceae (*Condalia ericoides*), as well as 2 sp. of Rutaceae (*Choysia dumosa*).

16. Sonoran-Chihuahuan: ranges in the Sonoran (+Mohavean) and the Chihuahuan (mostly western part) Subprovinces of the Sonoran Province (Figs. 6, 7). Of the 80 xerophytic species of this element, 18 sp. are in Asteraceae (*Acourtia nana*), while Sonoran wide element has only three species of this family. The 6 sp. of Cactaceae (*Mammillaria grahamii*), 5 each of legumes (*Dalea wrightii*) and ferns (*Cheilanthes villosa*), 4 sp. each of grasses (*Muhlenbergia arenacea*) and *Polygala* are followed by genera with 1–2 species (*Condalia viridis, Peganum mexicanum, Kallstroemia hirsutissima,* and *Salvia henrii*).

17. Chihuahuan: ranges in the Chihuahuan Subprovince including Edwards Plateau (Fig. 8). This richest in the flora geoelement has 253 species which reveals the high level of Chihuahuan endemism and diversification in temperate and tropical-subtropical genera. There are 44 sp. of Asteraceae, 24 sp. of cacti, 18 sp. of legumes, 15 sp. of grasses, 12 sp. each of Boraginaceae (mostly in *Heliotropium* and *Tiquilia*) and Brassicaceae, 8 sp. each of Nyctaginaceae and Lamiaceae, 7 sp. each of Agavaceae, Acanthaceae, and Euphorbiaceae, 6 sp. of Convolvulaceae, 5 sp. each of Fagaceae, Scrophulariaceae and Amaranthaceae, 4 sp. each of Caryophyllaceae, Solanaceae, Polemoniaceae, etc. There are fewer shrubs and small trees (*Ungandia speciosa, Diospyros texana, Leucophyllum minus, Holacantha stewartii,* and *Colubrina texensis*) but they dominate various types of xeric communities. Typical are the rosette forming lilioids (*Dasylirion leiophyllum, Nolina erumpens, Agave* and *Yucca*) and cacti (*Echinocereus, Escobaria,* etc.).

17a. North Chihuahuan: restricted to northern, mostly Unites States portion of the Chihuahuan Subprovince southward to Coahuila, Mexico. There are 35 sp. in this subelement (*Drymaria pachyphylla, Phyllanthus ericoides,* and *Hedeoma plicata*).

18. Chihuahuan-Tamaulipan: ranges in the Chihuahuan Subprovince extending eastward to the Tamaulipan Subprovince. Among 50 sp. of this geoelement 8 sp. are in Asteraceae, however they are of different genera than those of the chihuahuan element. The tropic/subtropical genera in this element are more pronounced (*Forestiera angustifolia, Guajacum angustifolium,* and *Passiflora tenuiloba*).

18b. Tamaulipan-Chihuahuan: ranges in the Tamaulipan Subprovince extending westward to the

Chihuahuan Subprovince. There are 5 sp. in this sub-element (*Agremone sanguinea, Cynanchum barbigerum, Ayenia pilosa, Meximalva filipes,* and *Thelesperma ambiguum*).

19. South Texas-Coahuila: a part of the Chihuahuan element with narrow ranges in SW Texas-(Edwards Plateau), and Coahuila-(Nuevo-Leon) of northern Mexico. This is an interesting group of 103 species (for example, *Lechea mensalis, Andrachne arida, Zanthoxylum parvum*) which deserves a separate analysis. A few subtypes are given below:

- **19a. South Texas Endemic:** mainly in Edwards Plateau extending to Trans-Pecos and along the Rio-Grande valley to N Tamaulipan Subprovince; 8 species (*Lithospermum mirabile, Chamaesyce angusta*).
- **19b. Trans-Pecos-Coahuila:** endemic or subendemic to Trans-Pecos and Coahuila; 29 species (*Quercus carmenensis, Fendlera rigida, Solanum leptosepalum, Eriogonum hemipterum, Phacelia robusta,* and *Selaginella viridissima*).
- **19c. Trans-Pecos (SW) Texas Endemic:** endemic to the Trans-Pecos region or parts of it; 29 species (*Prunus havardii, Eriogonum suffruticosum,* and *Selinocarpus parviflorus*).
- **19d. Brewster c Endemic:** endemic to the Brewster county or only Chisos Mountains; 10 species (*Hectia texensis, Quercus tardifolia,* and *Bouteloua kayi*).

TAXONOMETRIC ANALYSIS OF THE FLORA

1. FAMILIES

There are 1587 species in 592 genera, and 125 families of vascular plants in the Big Bend region flora. Most specious are cosmopolitan families Asteraceae (230 species/107 genera), Poaceae (202/63), and Fabaceae (107/37). They are listed first in the Tethyan (Saghatelyan 2006) floras as well, however, the first two families have as much as 30% of all species of the Big Bend flora. The leading position of Asteraceae reflects their South American origin (Funk et al. 2005) and outstanding diversity in Mexico (Rzedowski 1993; Turner & Nesom 1993; Valdés-Reyna and Cabral-Cordero 1993). The composition of legumes in the Big Bend flora is very different from that in the eastern Tethyan floras as exemplified by the flora Armenia (Saghatelyan 1997a,b; 2006). Unlike absolute dominance of temperate papilionoid legumes in Armenia, the Trans-Pecos flora has all three subfamilies well represented. Armenia has only *Cercis griffitii* of the basally branching Caesalpinioid legumes, the remaining genera being of more derived North Temperate papilionoid Hologalegina (Wojciechowski et al. 2000; Schrire et al. 2005). The Trans-Pecos flora has eastern North American *Cercis canadensis* and 6 genera/17 sp. of other basally branching clades of Caesalpinioideae (Schrire et al. 2005), mostly in Cassieae. Their ranges are in more subtropical latitudes and more eastern parts of the Madrean Region and eastern North America. Six genera and 27 species of the Mimosoideae in Trans-Pecos show only southern connections with the ranges mostly in different, especially the Chihuahuan, parts of the Madrean Region. Prevailing in North temperate floras Papilionoideae (62 sp. in Big Bend) are in the genera with mostly western ranges in North America (*Astragalus, Lupinus, Dalea, Sophora*). Fewer genera have mostly eastern North American ranges (*Lespedeza, Desmodium*), and a few have southeastern (*Rhynchosia, Indigofera*) ranges. According to classification of Schrire et al. (2005), the legume genera of succulent or temperate biome affiliation and amphiatlantic or pantropical disjunction prevail in the Big Bend region flora.

High diversity of the next two families, the American Cactaceae (59/17) and Euphorbiaceae (59/10) is due to the setting in the Sonoran Province, as well as (for Euphorbiaceae) on the southern border of the United States. The middle sized families—Brassicaceae (43/21), Cyperaceae (40/10), Lamiaceae (38/11), Boraginaceae (33/9), Solanaceae (32/10), Pteridaceae (33/8), Nyctaginaceae (32/13) Scrophulariaceae (29/13), Onagraceae (28/4), Malvaceae (24/12), Asclepiadaceae (23/4), Amaranthaceae (22/7), Chenopodiaceae (21/6), Verbenaceae (21/8), and Fagaceae (21/1)—reveal different connections: western and southern more than northern and eastern. The high position of Fagaceae is due to the proximity to the center of diversity of oaks in the highlands of central and eastern Mexico (Nixon 1993). If the Boraginaceae are counted with the western American Hydrophyllaceae (14/2), the combined 47 species would be in fifth place after Cactaceae/

Table 2. Major groups of genera of the Big Bend flora.

North Temperte Old World	19
Relictual North Temperte	30
American-African	20
Madro-Tethyan	5
East Gondwanan	5
North American	37
E N American	7
W N American	57
Amphitropical	10
Apachian	5
Chihuahuan	7
Madrean	4
Mega Mexico II	10
Mega Mexico III	26
SW N America	41
Tropic-Subtropical American	56
Tropic-Subtropical	47
Tropic-Warm Temperate	37
Tropical American	21
Tropical	6
Temperate-Subtropical American	7
Temperate-Subtropical North and South	9
Total	466

Table 3. Genera combined.

North Temperate (wide and relictual)	54
North Americn Genera (wide and east)	106
Madrean	98
Tropic/Subtropical/(Warm) Genera	212
West/SW/S North American Genera	122
American	288
Laurasian	160
Gondwanan	306

Euphorbiaceae by their importance in the xeric vegetation. The Boraginaceae (Eritricheae) are especially prominent in the California Province (Raven & Axelrod 1978), but also interesting in their geographical connections and tribal representation in the Big Bend. The disjunctive North Temperate Boraginoideae have 12 species of Eritricheae (*Cryptantha*, 9 sp.) and 7 sp. of Lithospermaeae (*Lithospermum*, 5 sp.) in the Big Bend flora. Only slightly fewer species of the Boraginaceae in the flora represent two tropical tribes, the Heliotropoideae (*Heliotropium*, 8 sp.) and Ehretioideae (*Tiquilia*, 5 sp.).

Paucity of species in typical North Temperate families like Caryophyllaceae (15/5), especially the older ones, like Rosaceae (12/9) and Ranunculaceae (11/7), is due to the young age of this xerophytic flora and its remoteness from eastern and western North American mountains. Among only 28 (!) species of petaloid, monocot families (by contrast richly represented in Armenia) all, except for a few species of *Allium*, have the Southern Hemisphere connections. In the Rhamnaceae (11/9) of the flora, the species of Madrean origin and southern connections prevail.

The remaining 44 families have 3–10 species each and contribute only 264 (13%) species to the flora. Sixteen families have only two species, and 27 families have only one species each. This type of spectrum illustrates an arid subtropical character of the flora of a recent age. It supports the inclusion of the Big Bend

Table 4. Western North American genera (+ W S North American). Numbers in parentheses: (total sp./sp. in Big Bend).

Fendlera (3/3 SW N Am)	*Giliastrum* (3/3 SW N Am)	*Stephanomeria* (24/2)
Nama (45/7)	*Ipomopsis* (24/5)	*Telesperma* (12/5)
Phacelia (200/9)	*Eriogonum* (250/15)	*Townsendia* (25/1)
Cryptantha (100/9)	*Schoenocrambe* (4/1)	*Xylorhiza* (8/1)
Poliomintha (4/1 SW N Am)	*Stanleya* (6/1)	*Trixis* (60/1 SW N Am)
Salazaria (1/1 SW N Am)	*Karwinskia* (17/1)	*Tridestomia* (7/4 SW N Am)
Dasylirion (1/1 SW N Am)	*Holodiscus* (8/1)	*Amsinckia* (50/1)
Nolina (15/2 SW N Am)	*Purshia* (7/1)	*Halimolobus* (15/2)
Cevallia (1/1 SW N Am)	*Nerisyrenia* (9/1)	*Cleomella* (10/1)
Eucnide (8/1 SW N Am)	*Aloysia* (58/2, to S America)	*Ribes* (150/3, temperate Eurasia, NW Africa)
Jamecia (12/1)	*Bahia* (15/4)	*Ibervillea* (5/2 SW N Am)
Rhynchosida (2/1)	*Encelia* (15/1)	*Dalea* (160/17, chiefly Mexico, SW N Am)
Sphaeralcea (60/6)	*Flourensia* (30/1)	*Lupinus* (200/3 +Mediterranean, trop. Africa)
Acleisanthes (7/3 SW N Am)	*Gutierrezia* (20–30/4)	*Escobaria* (16/8)
Selinocarpus (9/3)	*Helenium* (40/3)	*Blepharidachne* (4/1)
Camissonia (62/1)	*Heterosperma* (5/1)	*Hesperostipa* (1/1 SW N Am)
Papaver sect. Agremone (28/4)	*Hymenoxis* (28/1)	
Platystigma (9/4)	*Stevia* (230/2)	
Gilia (25/1)	*Macharanthera* (35/5)	

region in the natural chorion Mega-Mexico 2 (Rzedowski 1993), as well as its good placement in the Sonoran Province (Thorne 1993) and the Western Region (McLaughlin 2007) of North America.

2. GENERA

Proportions of major geographic groups of genera, except cosmopolitan, in the Big Bend flora are illustrated by Tables 2, 3, and 4. More than two thirds of the genera have their origins in different parts of the Americas. Together with tropic-subtropical genera, the majority of which are also American, 78% of all the genera are restricted to the Western Hemisphere. West-east connections across the Northern Hemisphere are much weaker. Only 25% of all genera belong to northern (warm) temperate flora, while tropic-subtropical genera comprise 37% and illustrate the essentially American and warm temperate-subtropical character of the Big Bend region flora that has much more connections with the south, than with the north. Rzedowski (1993) stated that in the entire Mexican flora the southern connections are four times stronger than the northern ones.

1. North Temperate Old World Genera.—This group of 19 genera has 50 native species in the Big Bend flora. These are *Allium* (700 world /6 Big Bend/ 102 USA), *Linum* (180/8/36), *Limonium* (350/1/10), *Centaurea* (500/1/4), *Filago* (35/1/3), *Lactuca* (100/2/8), *Daucus* (22/1/2), *Lappula* (60/1/2), *Lithospermum* (60/5/8), *Omphalodes* (28/1/3), *Erysimum* (100/2/20), *Noccaea* (13/1/5), *Silene* (500/3/79), *Bassia* (26/1/6), *Corispermum* (70/1/9), *Krasheninnikovia* (9/1/1), *Helianthemum* (110/1/14), *Astragalus* (2200/9/349), *Polypogon* (15/4/8), and *Arundo* (5/1/1). Eurasian (EA) origin is well known from their distribution and is supported by phylogenetic data for several genera, like *Linum* (McDill et al. 2008) and *Limonium* (Lledo et al. 2005). Eurasian origin and migration via the Bering Land Bridge (BLB) with consecutive single colonization event to Andean South America were stated for *Astragalus* (Scherson et al. 2008) and *Silene* (Popp & Oxelman 2007). The majority of the genera in this group are of the young Neogene age (Popov 1963), with recent migration events to North America (NA) and from there to temperate South America. Their centers of diversity lie in different parts of the Tethyan Subkingdom: for *Centaurea* in Western Asia, for *Silene* in the Eastern Mediterranean-Western Asia, for *Limonium* in the Mediterranean, while the largest papilionoid genus *Astragalus* is in the first place in any Irano-Turanian flora. The genus *Allium* has a huge center in the Tethyan Subkingdom and an essential one in western North America. Most of these genera probably reached the Big Bend region from the north-west (via the BLB), fewer genera (*Helianthemum*, *Linum*, and *Limonium*) more likely crossed the

Atlantic. Lledo et al. (2005) stated a close connection of the North American *Limonium* species with northern European species of recent, Pliocene, age and an earlier migration of one species of a different clade to South America. Thus, independent migrations of *Limonium* species from the Western Mediterranean to the Americas in the Middle Miocene and in the Pliocene time could illustrate the recent pattern of Madrean and Tethyan disjunctions, as opposed to that of older genera migrated earlier in the Tertiary in both directions (Manchester 1999; Tiffney & Manchester 2001; Tiffney 2000).

2. Genera of Northern Latitudes and Mountains.—This group has genera with wide north temperate distribution including those with arcto-alpine species. Many of them have their major center of diversity in Eastern Asia (EA.), for example, *Arenaria* (China 102/world 300/Big Bend 5), *Androsace* (73/100/2), *Anemone* (53/120/2), *Clematis* (147/300/2), *Delphinium* (173/350/2), *Salix* (275/520/5), and *Gentiana* (248/361/1). More diverse in North America are *Draba* (world 350/ NA 102/ China 50/Big Bend 3) and *Aquilegia* (world 70–100/ NA 22/China 13/Big Bend 2). In North America they are mostly found in the western half, especially the Rocky Mountains and Great Basin. A North American genus *Epilobium* (world 165/NA 42/Big Bend 1) has seven sections most diverse in the Madrean Region or restricted to it, with the large section *Epilobium* diversified in all other continents except Antarctica (Katinas et al. 2004).

3. Relictual Widely North Temperate Genera.—This is a group of relictual genera, disjuncts of Eastern Asian-Eastern North American, as well as several smaller southern Eurasian regions of preservation of the Tertiary Laurasian flora. These are *Juglans* (world 21/Big Bend 2), *Fraxinus* (65/4), *Crataegus* (265/1), *Prunus* (430/3), *Ostrya* (7/1), *Lonicera* (200/1), *Vitis* (65/1), *Viburnum* (225/2), *Philadelphus* (75/4), *Cercis* (6/1), *Pseudotsuga* (6/2), and *Lespedeza* (40/1). It was suggested that *Juglans*, *Fraxinus*, and *Acer* have North American origin in the Eocene (Manchester 1999), while *Lonicera* and *Viburnum* (Bell & Donoghue 2005), as well as *Mahonia* (Wang et al. 2007) have E Asian origin and BLB crossing. *Symphoricarpos* (20/2) is mostly a NA genus with only one species in EA. *Pinus* (100/3) and *Mahonia* (110/2/) have more species in the Western, than the Eastern Region of North America. Together 30 north temperate genera of groups 2 and 3 have only 60 species (4%) in the Trans-Pecos flora. They occur mostly at higher elevations or are scattered on the canyon walls and along rivers (Powell 1998).

4. Widely Distributed Temperate Old World-New World Genera.—A group of 21 large genera of different (mostly Laurasian) origin widely distributed in temperate regions of both North and South Hemispheres. There are 80 species of the flora in these genera. Some of them have two centers of diversity: in Asia and in Mexico. The latter center is reflected in the Trans-Pecos flora by the high numbers of species in *Quercus* (500 world/150 Mexico/20 Big Bend), *Salvia* (900 world/325 Mexico/12 Big Bend/84 China/46 Ecuador, and a big center in Irano-Turania), and *Lithospermum* (60 World/5 Big Bend). A great antiquity and Laurasian affinities for Mexican *Salvia* were stated by Ramamoorthy (1993). Other genera have a big center in Asia and one (via the Beringian crossing) in western North America (*Artemisia*: 300 World/ 200 China/ 58 United States/5 Big Bend), or in Asia and in the Appalachian and Rocky Mountains (*Thalictrum* (150 world/73 China/ 23 US). Fewer genera of this type are of North American origin: *Solidago* (100 world/5 Big Bend/ 72 US/ 5 China). The remaining genera are almost cosmopolitan: *Marrubium*, *Lamium*, *Mentha*, *Stachys*, *Polemonium*, *Hieracium*, *Bromus*, *Poa*, *Rhamnus*, *Paronychia*, and others.

5. North American Genera.—This group has 37 genera/91 species (5.8% of the flora) of North American and 7 genera/11 species of Eastern North American (*Liatris*, *Ratibida*, and *Spermolepis*) origin. Most of them are of herbaceous habit and many are from Asteraceae. The larger genera have up to 8 sp. in the Big Bend flora (*Penstemon*: 265 total /8 Big Bend; *Erigeron*: 200/8; and *Castilleja*: 200/4). The smaller genera have 3 to 6 sp. in the region (*Matelea*: 150/4, *Lesquerella*: 40/6, *Helianthus*: 49/4, *Packera*: 67/3, *Gaillardia*: 28/4, and *Gaura*: 21/6).

6. Western North American Genera.—Table 4 has a list of 57 indigenous western NA wide genera that are very important in the plant cover. These genera contribute 170 species (10.6%) to the flora. This group should include as well 12 species of five small, but peculiar Apachian genera (*Fallugia*, *Engelmannia*, *Pseudoclappia*, *Fendlera*, and *Berlandiera*) and seven monotypous Chihuahuan genera (*Amblyolepis*, *Psathy-*

rotopsis, Emorya, Ariocarpus, Lophophora, Allolepis, and *Holacantha*). The Trans-Pecos flora has four of the renouned Madrean genera: *Foquieria, Chilopsis, Wislizenia,* and *Nectouxia*. Altogether there are 73 western North American genera with 193 sp. in the flora.

7. Amphitropical Genera.—There are 23 species of 10 amphitropial genera in the flora: *Krameria*: 18 total/3 Big Bend; *Larrea*: 5/1; *Tiquilia*: 20/5; *Koeberlinia*: 1/1; *Hoffmanseggia*: 28/3; *Gottea*: 1/1; *Trichloris*: 2/1; *Hedeoma*: 38/7; and *Scleropogon*: 1/1. They grow in warm arid and semiarid regions of temperate North and South America and have different evolutionary patterns involving long distance dispersals. For example, Simpson et al. (2004) stated that *Krameria* has two major clades each containing a North and a South American subclade. They result from two independent dispersals, or two vicariant episodes, involving North and South America. *Hoffmanseggia* arose in South America and had at least two dispersals to North America at different times (Simpson et al. 2005). *Tiquilia*, as stated by Moore and Jansen (2006), exhibits a North American origin and first divergence after greatest Cenozoic episode of rapid aridification near the Eocene/Oligocene boundary, major diversification in the NA deserts in the Miocene and four long distance dispersals to South America (Moore et al. 2006). The monotypic genus *Koeberlinia* of core brassicalean affinity is of North American deserts origin (Tobe & Raven 2008). For the American *Larrea* clade a separation from Old World *Zygophyllum* by sea floor spreading in the Cretaceous was proposed (Porter 1972; Sheahan & Chase 1996). The South American-North American Larreoideae has two out of the five genera in the Big Bend flora. Sheahan and Chase (2001) stated that they are of South American origin and recent, Late Neogene, time of arrival by long distance dispersal of the ancestors of *L. tridentata* to North American deserts.

Altogether, 82 western American genera with 204 sp. (14% of the flora) in groups 6 and 7 represent the core of the autochthonous xeric floristic complex of the south-western deserts in the Big Bend region flora. Many dominant and co-dominant species of the genera like *Foquieria, Larrea, Koeberlinia, Nolina, Dasylirion, Aloysia, Fallugia,* and others, are in these two groups. Most of them arose from the ancestors of Madro-Tertiary geoflora (Axelrod 1975; Raven & Axelrod 1978) affiliation. Fewer genera, for example, *Eriogonum, Nerisyrenia* and section Argemone of *Papaver,* are Cenozoic western North American (Madrean) derivatives of the ancestors from Arcto-Tertiary geoflora.

8. American-African Genera.—There are 20 genera with 57 sp. disjunctly distributed in America and Africa: *Thalinum, Thamnosma, Mimulus, Ambrosia, Coreopssis, Flaveria, Asclepias, Lupinus, Pomaria, Parkinsonia, Heteranthera, Sageretia, Sideroxylon, Nicotiana, Bouchea, Lantana, Tagetes, Calliandra, Galactia, Mimosa,* and *Sorgastrum*. Some of them, like *Mimosa* (6 sp.), *Asclepias* (12 sp.), *Lupinus* (3 sp.) and *Nicotiana* (3 sp.) are more specious in Big Bend and important in the plant cover. Transatlantic disjunctions of this group at the genus level were attributed to long-distance dispersal in both directions mostly by water, while species level disjunctions, to the anthropogenic factor (Renner 2004; Pennington et al. 2006; Simpson et al. 2006).

9. Madro-Tethyan Genera.—There are only 5 genera and 9 species that can be defined as Madro-Tethyan in the Big Bend flora. Some of those analyzed by Axelrod (1975), for example *Pistacia*, are not in the region, but grow not far from it, in the mountains of eastern-southern Mexico. Others, like *Quercus, Juniperus,* and *Pinus*, were considered in the group 3 or 4 of this classification, even though they have entire vicariant sections in the Tethyan and Madrean mountainous vegetation of low-middle altitudes. Some genera of Madro-Tethyan origin have a wider range today (e.g., *Cercis*). Because the present scheme follows contemporary ranges of taxa, these genera have been included in group 4 of north temperate relicts. Basalmost Cesalpinioideae was important in the Tertiary floras of subtropical littoral type (Mai 1995) and *Cercis* is in the Mediterranean element of many authors (Mai 1987; Kamelin 1983). In many cases, a convergent character of the Madrean and Tethyan similarities, much discussed in the literature (Axelrod 1975; Raven 1971, 1973), stems from the old age of such madro-tethyan genera. "The closer correspondence of woody taxa between the Madrean and Tethyan regions in the Tertiary time stems chiefly from a more favorable climate and terrain for a wider distribution" (Axelrod 1975:316).

The five Madro-Tethyan genera in the Big Bend flora are as follows:

Ephedra—35–70 extant species in Central and SW Asia, SW North America, Mexico, Mediterranean,

N Mediterranean Africa, and Andes from Ecuador to Patagonia. Four species grow in Trans-Pecos. Rydin et al. (2006) stated a striking increase in gnetalean diversity and wide distribution of *Ephedra* and *Ephedra*-like plants across Laurasia in the Early Cretaceous followed by a significant decline through the Late Cretaceous. Major groups of *Ephedra* originated after the final rifting of Gondwana (Rydin et al. 2004) and have good pollen record in Early Cretaceous paleoequatorial regions of Africa-South America (Crane 1996). Early Cretaceous fossils from Brazil, USA (Virginia), China, and Portugal very similar to extant *Ephedra*, suggest that crown group of *Ephedra* might be of Mesozoic origin (Rydin et al. 2004). North African-Mediterranean species are in a basal grade whereas all non-African species belong to a clade of Asian origin and New World species originated within the Asian clade (Rydin et al. 2004). Major center of diversity of extant Ephedra is in Central Asia (18 sp.) with pollen recorded for SW Siberia since the Upper Cretaceous (Peshkova 2005). Presence of an arid center in continental Asia since the Upper Carboniferous was stated by Kryshtofovich (1955). "Apparently, the same flora of Angarida or Tungussian Flora is ancestral to both the Permian xeric flora of Europe and Jurassic polichronous flora with its mesophytic characteristics. In the Upper Permian and Lower Triassic extensive orogenesis and lava intrusions in Asia brought about even larger expansion of the arid territories around the dry core of Asia" (Kryshtofovich 1957:46–47; cited and translated from Peshkova 2005).

Cupressus—28 taxa, 16 in W USA, Mexico to Central America, the rest in NW Africa, Middle East along Himalaya to SW and Central China (4 species) and N Vietnam (The Gymnosperm database). Recent phylogenetic research (Little 2006) stated the polyphyly of *Cupressus* with the 12 Old World species being sister to *Juniperus*. The 16 New World species of *Cupressus* plus *Callitropsis* were resolved as sister to the Old World *Cupressus* plus *Juniperus* clade.

Arbutus—14–20 sp., W North America, Central America, West Europe, Mediterranean, and SW Asia. A Laurasian origin for Ericaceae in the Late Cretaceous with the Arbutoideae in the basal clade was stated by Kron and Luteyn (2004). "A widespread common ancestor may have occurred along the coastline of the developing Tethyan seaway and subsequent vicariance may have been a major factor in the initial divergence of the ancestors of Arbutoideae, Ericoideae, and Vaccinioideae due to the continued drifting apart of Africa, Europe, and North America" (Kron & Luteyn 2004:498). The diversification of Arbutoideae along the Tethys seaway stated also by Hileman et al. (2001) might explain the contemporary disjunctions and is reminiscent of the pattern in other older Madro-Tethyan genera, like *Ephedra, Cercis, Cupressus,* pinions, and evergreen oaks.

Oligomeris—3 species, two of which are SW African, one *O. linifolia* from N Africa to W India, Canary Islands and southern and south-eastern United States and Mexico, all growing in desert vegetation (Kubitzki 2003). Resedaceae, an Old World family of Capparalean affinities (Kubitzki 2003), has 6 genera and ca. 85 sp., with a major center of diversity in the arid regions of the Mediterranean basin and two centers of differentiation, one in the western Mediterranean, and the other in the eastern Mediterranean and SW Asia (Martin-Bravo et al. 2007). It might have crossed the Atlantic by long distance, as the access to post Eocene NALB was restricted to cool-temperate and deciduous taxa (Tiffney 2000). Other younger Tethyan groups since the Neogene time with concentration in the Mediterranean basin (like Cistaceae and Limoniaceae) follow a similar pattern. Latest phylogeographic analysis also stated for *Oligomeris* a long-distance dispersal event from the Old World during the Quaternary (Martin-Bravo et al. 2009).

Peganum—5–6 species in the Mediterranean, southeast Europe, Transcaucasia, Middle Asia, Iran, Afghanistan, Mongolia, China, India; one species in eastern and north-central Mexico. Recent placement of Peganaceae in Nitrariaceae (Angiosperm Phylogeny Website) along with other Eastern Tethyan (Irano-Turanian) genera, *Nitraria* and *Malacocarpus*, makes the Tethyan origin of *Peganum* even more obvious.

10. Mega-Mexico II Genera (Rzedowski 1993).—Ten genera with 21 species of the flora have their ranges in Mexico and southern United States. All of them belong to Asteraceae, Cactaceae, and Poaceae.

11. Mega-Mexico III Genera (Rzedowski 1993).—Twenty six genera and 58 species have their ranges in Mexico, extending to southern United States as well as tropical Central and northern South America. Among them are *Agave* (100/, Agavaceae), *Echeandia* (12/1, Asphodellaceae), *Pilostiles* (25/1, Rafflesiaceae),

(*Bouwardia*, 20/1, Rubiaceae), *Leucophyllum* (12/3, Scrophulariaceae), 8 small asteraceous genera, and one of each family Cactaceae, Poaceae, and Amaranthaceae. Three small genera are present also in the West Indies: *Maurandella* (Scrophulariaceae), *Jefea* (Asteraceae), and *Garrya* (13/2, Garryaceae). Among the three Mesoamerican genera *Hechtia* (47/1, Bromeliaceae) extends northward to only 3 counties of southern Texas in the United States.

Altogether, there are 23 genera with 68 species of groups 10 and 11 in the Big Bend flora. Species of some of them (like *Agave, Leucophyllum, Garrya,* and *Echinocereus*) play a dominant role in the xeric communities of the Madrean vegetation.

12. Western and south-western United States, Mexico (northern) and Texas (southern United States) Genera.—Forty one peculiar genera with 70 sp. evolved in the Madro–Tertiary Geoflora have this type of range. Among those, six genera of the Cactaceae are most diverse. The remaining genera are from mostly tropical–warm temperate families like Apocynaceae (*Haplophyton*), Malvaceae (3), Nyctaginaceae (3), Rhamnaceae (*Adolphia*), Solanaceae (*Chamaesaracha*), and Verbenaceae (*Tetraclea*); largely tropical Rutaceae (*Choisya, Ptelea*) and Sapindoideae (*Ungandia*). The Asteraceae have 12 genera, papilionoid legumes have three, and endemic western North American family Crossosomataceae is monotypic. Prevalence of warm temperate-subtropical-tropical connections, some of those being very interesting, is evident from this list. For example, in core Rutaceae (Groppo et al. 2008) *Choisya* (4–5) and *Ptelea* (1–3) form a tropical American clade, *Zanthoxylum* is pantropical, and *Casimiroa-Dictamnus* clade has *Dictamnus* (1–2 sp. S Europe to N China), *Skimmia* (4 sp. east of the Himalayas to S Vietnam and the Philippines) and *Casimiroa* (Mexico, Costa Rica). Thus, core Rutaceae clade exemplifies both Madrean-tropical American connections and east to west Old World-New World (madro-tethyan) connections along the southern Tethys shore.

Among primarily north temperate families, the Brassicaceae has two and the Rosaceae has three genera (*Cercocarpus, Malacomeles,* and *Vaquelinia*) which exhibit this pattern of distribution. Six of the eight rosaceous genera in Trans-Pecos arose in the Madro-Tertiary Geoflora, with the remaining two genera being in common with the Old World.

13. Tropic-Subtropical American Genera.—There are 56 genera (119 sp.) in the flora with large distribution in tropical and subtropical parts of the Americas. Some of those are very peculiar and important in xeric desert and thorn shrub communities (*Condalia, Holocantha, Guajacum, Calliandra, Proboscidea, Mentzelia, Eryngium*, etc). The largest family in this group is Asteraceae (12 gen.).

14. Tropic-Subtropical Genera.—There are 47 genera (102 sp.) of pantropic-subtropical distribution in Trans-Pecos. The grasses (10 gen.) and the legumes (8 gen.) are most specious, including some dominant species (*Acacia*, 9 sp., *Prosopis*, 2 sp). Several Euphorbiaceae (4 gen.), like *Jatropa*, have interesting disjunctions; the same refers to the Rhamnaceae (*Colubrina, Ziziphus*) and *Buddleja*. The genus *Boerhavia*, Nyctaginaceae, has 8 out of its 20 species in the Big Bend flora.

15. Tropical to Warm Temperate Genera.—There are 42 tropic/subtropical genera (179 sp.) extending to warm temperate countries in the flora. The majority of them are grasses with 15 gen. /83 sp. (*Imperata, Pappophorum*, etc.), followed by Malvaceae (4/11), Cyperaceae (3/18), Amaranthaceae (2/12), *Senna* (10), *Heliotropium* (8), *Ipomoea* (8), *Kallstroemia* (5), and *Rhus* (4).

16. Mostly Tropical American Genera.—Twenty one genera with 64 species. Here are the legumes (4 gen./7 sp.), Cucurbitaceae (2 gen.), and others (*Tecoma, Tillandsia*). Eleven more genera and 50 sp. have wider distribution in the Americas, are important in the plant cover, and have their ranges centered primarily in Central and South America (*Baccharis*, 6 sp; *Opuntia*, 16 sp; and *Bouteloua*, 15 sp.).

17. Tropical genera.—Six genera with 10 sp. of pantropical distribution: *Cissus, Sesuvium, Rynchosia*, and three genera of the grasses.

18. Temperate-Subtropical American Genera.—Seven American genera with 41 sp. are widely distributed in north and south temperate and subtropical latitudes: *Oenothera* (11), *Verbena* (7), *Physalis* (6), etc.

19. Temperate-Subtropical Genera of North and South Hemispheres.—Nine genera with 21 species absent from the tropics have this type of wide distribution. Five of them are grasses (*Agrostis, Melica*, and

Hordeum). Most specious in this group is *Lycium* (5 sp). It has 70 species disjunctly distributed in temperate subtropical regions of South and North America, S Africa, Australia, and Eurasia. Fukuda et al. (2001) stated that *Lycium* originated in the New World, all the South African, Australian, and Eurasian species together are monophyletic and have a common ancestor from the New World. It was confirmed by recent data (Levin & Miller 2005) that the Old world *Lycium* species clade is nested within the American species, which comprise the rest of the Lycieae. This is another example of Madro-Tethyan connections, although the genus has a wider distribution. Species of *Lycium* grow in littoral (turgay) communities of dry regions in the Tethyan subkingdom.

20. Leptopus phyllantoides, tribe Poranthereae, Euphorbiaceae presents an interesting case.—An endemic NA clade of *Andrachne* section *Phyllanthopsis* (Vorontsova et al. 2007) includes two species disjunctly distributed in Trans-Pecos-Coahuila, Edwards Plateau and Ozarks Plateau. It is a relictual disjunctive type of range. This clade is sister to a clade of mesophyllous shrubs restricted to relictual humid forests of western Transcaucasia, Asia, and Indonesia plus a clade of evergreen rainforest understory trees of Asia and Australia (Vorontsova et al. 2007). These authors state that tribe Poranthereae appears to be centered in Africa, with movement to Asia, Australia, and the New World, and movement from subtropical arid habitats to wetter temperate and tropical ones. The basalmost clade combines microphyllous procumbent species of semi-deserts and has two subclades: the African-American (Somalia, Ethiopia/Mexico, and Peru) and the Asian/ African subclade (Horn of Africa and N Africa/ Irano-Turania). The New World subclade of the basalmost clade indicates a single colonization and has two very similar amphitropical species of *Andrachne* in Baja California and Peru. Thus, we see another example of colonization of North America from both the northern route across Laurasia (section *Phyllanthopsis*), and along the southern Tethys shore across the Atlantic (the Mexican-Peruvian species).

This latter migration track seems very feasible for termophyllous ancient taxa originated or preserved in the Horn of Africa region. The importance of that region was stated by many researchers of Africa: "The high endemism of Horn of Africa emerges clearly....The flora of the Somali Republic is a remarkable one with very many outstandingly distinct species found nowhere else" (Brenan 1978:467). "The Somalian phytochorion could be seen as a hub for the arid truck" (Thulin 1994). "In historical terms it suggests that Horn of Africa would be a refuge area for the arid flora" (Friis & Balsev 2005).

The rest of the genera are cosmopolitan, or of wide temperate distribution, or have mostly non-native species in the flora.

CONCLUSIONS

The setting of the Big Bend region flora on the boundary of two subkingdoms of the Holarctic Kingdom explains its mixed character with combination of lineages evolved either from Madro-Tertiary or Arcto-Tertiary geoflora stock. However, the Madrean lineages predominate and the flora is mostly south-western North American by composition (Table 1). There are 1586 native species in 595 genera of 125 families in the Big Bend region flora. Many genera and families in the flora are monotypic or oligotypic.

Three quarters of the genera are restricted to the Western Hemisphere, and tropic/subtropical, mostly South American, genera have 37% of the species diversity in Trans-Pecos. Taxa with southern connections, especially the Madrean element which has 1056 species (or 66%) of the flora, prevail. The Chihuahuan Subprovince has a high level of endemism (26% of the flora) with many younger taxonomic groups, evolved in situ since the Cenozoic rapid aridification episode. It is well placed in the Sonoran Province, however, its boundary with the Tamaulipan Subprovince is very vague.

North Madrean and southern Rocky Mountains-Sonoran species (6% of the flora) are of either Madro-Tertiary or Arcto-Tertiary geoflora affiliation. The Apachian element is well represented (9% of the flora) which corroborates delineation of the namesake subprovince (McLaughlin 2007), while the Comanchian (2.5% of the flora) probably is a chorion of a lower rank.

East to west connections across the northern Hemisphere have a lesser weight in the flora. The older

Laurasian genera that migrated in the early Tertiary via one of the two northern bridges are not many in this younger flora. The NA-EA similarities are on the genus level and above. More recently migrated to the region are mostly progressive eastern Tethyan (mostly Irano-Turanian) genera which came from Asia via the BLB (Salsoleae, *Astragalus*).

Diversification of older Madro-Tethyan genera, like *Ephedra, Cercis, Arbutus, Cupressus*, pinions, and evergreen oaks along the Tethys seaway and recent long distance dispersal of younger genera from the Mediterranean (*Oligomeris, Limonium*) might explain contemporary pattern of the Madrean and Tethyan disjunctions. Another pattern (core Rutaceae) shows both Madrean-tropical American connections and Old World-New World connections along the Tethys shore. The southern east to west connections across the Atlantic along the southern Tethys shore are evident from several striking examples in Zygophyllaceae, tropical Boraginaceae, Rutaceae, succulent biome Fabaceae, Euphorbiaceae, Agavaceae/Dracenaceae and others.

APPENDIX 1

AREA DIAGNOSES FOR THE SPECIES OF BIG BEND REGION, TEXAS

The following list of species was extracted mostly from the Synthesis of the North American Flora (Kartesz & Meacham 2002) and it follows, with few exceptions, all the nomenclatural combinations as well as author citations of this source. The nomenclature and distributional data of the Onagraceae follows the Onagraceae website (Wagner & Hoch 2005) and the *Leptopus* clade follows Vorontsova et al. (2007). In the few cases where the nomenclature is different from that in the above mentioned sources, the author names are cited. The list below should be considered as a compilation for the purposes of areal descriptions rather than a comprehensive checklist. The families of vascular plants are arranged in the alphabetical order as are genera and species. Numbers by each family name indicate species/genera ratios in the family.

ACANTHACEAE: 18/8
Anisacanthus linearis Chihuahuan
Anisacanthus puberulus Chihuahuan
Anisacanthus quadrifidus Chihuahuan
Carlowrightia arizonica Sonoran
Carlowrightia linearifolia Apachian
Carlowrightia mexicana Tr-Pecos-Coahuila
Carlowrightia parvifolia Tr-Pecos-Coahuila
Carlowrightia serpyllifolia Tr-Pecos-Coahuila
Carlowrightia texana Chihuahuan
Dyschoriste linearis SC US
Dyschoriste schiedeana Sonoran-Chihuahuan
Elytraria imbricata Mesoam-Madrean
Justicia pilosella Chihuahuan-Tamaulipan
Justicia warnockii Tr-Pecos
Ruellia corzoi Chihuahuan
Ruellia parryi Chihuahuan
Stenandrium barbatum Chihuahuan
Tetramerium nervosum Sonoran

ACERACEAE: 1/1
Acer grandidentatum N Madrean Mont. (S Rocky M-E Great Basin-Sonoran Province)

AGAVACEAE: 10/2
Agave glomeruliflora Chihuahuan
Agave gracilipes Chihuahuan
Agave havardiana Tr-Pecos Endemic
Agave lechuguilla Chihuahuan
Agave parryi Sonoran
Yucca baccata SW US
Yucca elata Sonoran-Chihuahuan
Yucca faxoniana Chihuahuan
Yucca thompsoniana Chihuahuan
Yucca torreyi Chihuahuan

AIZOACEAE: 1/1
Sesuvium verrucosum American Trop/Subtr

ALISMATACEAE: 1/1
Sagittaria calycina N American

AMARANTHACEAE: 22/7
Alternanthera caracasana Tropical American
Amaranthis acanthochiton Chihuahuan
Amaranthus albus Polichorous
Amaranthus arenicola Prairie with radiations
Amaranthus blitoides N American (WC)
Amaranthus crassipes Caribbean
Amaranthus palmeri N American (SWC)
Amaranthus polygonoides Caribbean
Amaranthus powellii Cordilleran
Amaranthus retroflexus N American (polychorous)
Amaranthus scleropoides Chihuahuan-Tamaulipan
Amaranthus torreyi W Sonoran
Froelichia arizonica Sonoran-Chihuahuan
Froelichia gracilis N American
Gomphrena nitida Sonoran wide
Guilleminea densa Madrean
Iresine heterophylla Sonoran wide
Iresine leptoclada Chihuahuan
Tidestromia carnosa Chihuahuan
Tidestromia gemmata Chihuahuan
Tidestromia lanuginosa SW & SC US
Tidestromia suffruticosa Chihuahuan

ANACARDIACEAE: 4/1
Rhus lanceolata SC US-Chihuahuan
Rhus microphylla Sonoran-Chihuahuan wide
Rhus trilobata W N American (+ W Prairie)
Rhus virens E Madrean

ANEMIACEAE: 1/1
Anemia mexicana Mesoam

APIACEAE: 7/5
Ammoselinum popei S Prarie
Cyclospermum leptophyllum S N American
Daucus pusillus N American
Eryngium heterophyllum W & S Madrean
Eryngium leavenworthii S Prairie
Spermolepis echinata S N American
Spermolepis inermis C & S Prarie-Appalachian

APOCYNACEAE: 8/4
Amsonia longiflora Chihuahuan
Amsonia palmeri N Sonoran Province
Apocynum cannabinum N American
Haplophyton crooksii N Sonoran-Chihuahuan
Telosiphonia hypoleuca J Davis c, Madrean Mont
Telosiphonia lanuginosa Madrean Mont (East)
Telosiphonia macrosiphon Tr-Pecos-Coahuila

ARALIACEAE: 1/1
Aralia racemosa ssp. bicrenata SW N American

ARISTOLOCHIACEAE: 2/1
Aristolochia coryi S TX Endemic (SW-SC TX)
Aristolochia wrightii Chihuahuan

ASCLEPIADACEAE: 23/4
Asclepias asperula SWC N American
Asclepias brachystephana Sonoran-Chihuahuan
Asclepias engelmanniana Prairie-SWC US
Asclepias glaucescens (Sonoran)-Mesoam
Asclepias latifolia S Prairie–SW US
Asclepias nummularia Sonoran Subprovince
Asclepias oenotheroides SC US-Mesoam
Asclepias scaposa Chihuahuan disjunct ?
Asclepias sperryi Tr-Pecos-Coahuila
Asclepias subverticillata SW US-Chihuahuan
Asclepias texana N Chihuahuan-Coahuila
Asclepias viridiflora N American
Cynanchum barbigerum Tamaulipan
Cynanchum pringlei Chihuahuan
Cynanchum racemosum N Chihuahuan-Tamaulipan
Funastrum crispum SWC US-Chihuahuan
Funastrum cynanchoides N & W Madrean
Funastrum torreyi Chihuahuan-Tamaulipan
Matelea parvifolia N Madrean
Matelea producta N & W Madrean
Matelea reticulata Chihuahuan-Tamaulipan
Matelea texensis Tr-Pecos Endemic
Matelea sagittifolia S TX Endemic

ASPLENIACEAE: 3/1
Asplenium palmeri J Davis c. Mesoam-Madrean Mont
Asplenium resiliens N American
Asplenium trichomanes J Davis c. Holarctical

ASTERACEAE: 230/107
Acourtia nana Sonoran-Chihuahuan
Acourtia runcinata Chihuahuan-Tamaulipan
Acourtia wrightii Sonoran-Chihuahuan
Ageratina herbacea Madrean (SWC US)
Ageratina rothrockii Sonoran-Chihuahuan
Ageratina wrightii Chihuahuan
Amblyolepis setigera Chihuahuan-Tamaulipan
Ambrosia confertiflora SW & SC US. N Madrean
Ambrosia psilostachya N American-Mesoam
Amphiachyris dracunculoides Prairie
Aphanostephus ramosissimus ?
Aphanostephus riddellii SC US (W TX-Chihuahuan)
Artemisia campestris Holarctical
Artemisia carruthii SWC N American
Artemisia dracunculus Holarctical
Artemisia filifolia WC US
Artemisia ludoviciana N American
Astranthium robustum Tr-Pecos Endemic
Baccharis bigelovii Chihuahuan
Baccharis havardii Chihuahuan
Baccharis pteronioides Madrean wide
Baccharis salicifolia American Trop/Subtr
Baccharis salicina Prairie. WC N American
Baccharis wrightii SW N American
Bahia absinthifolia Sonoran-Chihuahuan
Bahia bigelovii Tr-Pecos Endemic
Bahia dissecta WC US Mont (Rocky M)
Bahia pedata S Rocky M-Chihuahuan
Baileya multiradiata Madrean (no Mexican Highlands)
Berlandiera lyrata Madrean
Bidens bigelovii SWC US-N Chihuahuan ?
Bidens laevis American Trop/Subtr
Bidens leptocephala Apachian
Borrichia frutescens Pecos c. Atlantic&Gulf Coast
Brickellia californica W N American
Brickellia conduplicata Chihuahuan Mont
Brickellia coulteri W Sonoran Province
Brickellia eupatorioides N American (not Pacific)
Brickellia grandiflora W N American
Brickellia hinckleyi Tr-Pecos Endemic
Brickellia laciniata Chihuahuan wide
Brickellia veronicifolia Chihuahuan-Mexican Highlands
Calyptocarpus vialis Mesoam-Gulf Coast
Carminatia tenuiflora Madrean Mont
Carphochaete bigelovii N Sonoran-Chihuahuan
Centaurea americana SW-SC US (S Prairie-Apachian)
Chaetopappa bellioides Chihuahuan-Tamaulipan
Chaetopappa ericoides WC N American
Chaetopappa parryi Chihuahun-Tamaulipan
Chaptalia texana E Madrean Mont
Chloracantha spinosa Mesoam-Madrean
Chrysactinia mexicana E Madrean Mont
Cirsium ochrocentrum WC US
Cirsium texanum Comanchian
Cirsium turneri S TX-Coahuila Endemic
Cirsium undulatum WC N American (Prairie-W US)
Conoclinium dissectum Chihuahuan
Conyza canadensis American
Coreopsis tinctoria N American
Cosmos parviflorus Apachian-Mexican Highlands
Dyssodia papposa Mesoam-N American

Eclipta prostrata American with radiations
Encelia scaposa N Chihuahuan
Engelmannia peristenia S Prairie-(S Rocky M-Chihuahuan)
Ericameria laricifolia N Madrean
Erigeron bellidiastrum WC N American
Erigeron bigelovii Chihuahuan
Erigeron colomexicanus ?
Erigeron divergens W N American
Erigeron eximius J Davis c. WN American Mont (Rocky M-Colorado-Apachian Mont)
Erigeron flagellaris W N American Mont
Erigeron modestus SWC US ?
Erigeron versicolor ?
Evax verna SC US (S Prairie)
Flaveria trinervia Mesoam with radiations
Flourensia cernua Sonoran wide
Flyriella parryi (ES) Chihuahuan
Gaillardia multiceps ?
Gaillardia pinnatifida SW US (not Cal)
Gaillardia pulchella N American (mostly S-C)
Gaillardia suavis S Prairie
Galinsoga parviflora American
Grindelia arizonica Apachian
Grindelia grandiflora J Davis c. N Chihuahuan
Grindelia havardii SW TX & SW AZ Endemic
Grindelia nuda SWC US
Grindelia oxylepis S Chihuahuan-(Mexican Highlands)
Grindelia scabra N Chihuahuan
Gutierrezia microcephala Madrean (no Mexican Highlands)
Gutierrezia sarothrae W N American
Gutierrezia sphaerocephala Chihuahuan-Tamaulipan
Gutierrezia texana Comanchian-Chihuahuan
Gymnosperma glutinosum Mesoam
Haploesthes greggii SW Prairie-Chihuahuan
Hedosyne ambrosiifolia Sonoran-Chihuahuan
Helenium amarum E N American
Helenium elegans Comanchian-Chihuahuan-Tamaulipan
Helenium microcephalum S Prairie-Chihuahuan-Tamaulipan
Helenium microcephalum var. *ooclinium* Chihuahuan
Helianthus annuus N American-Polichorous
Helianthus ciliaris SC N American
Helianthus niveus Sonoran proper (W Madrean)
Helianthus paradoxus Pecos, Reevs cc. ?
Heliomeris longifolia Madrean disjunctive
Heliomeris multiflora Rocky M
Heliopsis parvifolia N Madrean Mont
Heterosperma pinnatum Mesoam-Madrean
Heterotheca canescens SC-SW Prairie
Heterotheca fulcrata W US Mont
Heterotheca subaxillaris N American
Heterotheca villosa W N American
Heterotheca viscida N Chihuahuan (+ S AZ)
Hieracium carneum S Great Basin-N Chihuahuan (+ S AZ) Mount disjunctive
Hieracium schultzii Mesoam
Hymenoclea monogyra N Madrean
Hymenopappus flavescens SW US
Hymenopappus scabiosaeus Prairie
Hymenoxys odorata SW Prairie-N Madrean
Isocoma pluriflora Chihuahuan
Iva angustifolia J Davis c. ?
Jefea brevifolia Chihuahuan
Koanophyllon solidaginifolium Chihuahuan
Lactuca graminifolia Apachian (SW US)
Laennecia coulteri N Madrean
Laennecia filaginoides Mesoam-S American
Laennecia sophiifolia Amphitropical ?
Leuciva dealbata Chihuahuan
Liatris punctata Prairie
Lygodesmia ramosissima Sonoran-Chihuahuan
Lygodesmia texana S Prairie-Chihuahuan
Machaeranthera blephariphylla N Chihuahuan ?
Machaeranthera gracilis N Madrean
Machaeranthera gypsophila Chihuahuan
Machaeranthera pinnatifida Prairie-Madrean
Machaeranthera tanacetifolia W Prairie-S Rocky M-Madrean
Melampodium leucanthum SWC US
Melampodium strigosum J Davis c. Sonoran-Chihuahuan ? (+ Colorado)
Nicolletia edwardsii Chihuahuan
Packera millelobata Chihuahuan
Packera neomexicana Apachian
Packera plattensis J Davis c. EC Prairie
Palafoxia callosa Comanchian extending to MO
Palafoxia riograndensis Chihuahuan
Palafoxia sphacelata E Prairie
Parthenium argentatum Chihuahuan-Mexican Highlands
Parthenium confertum Chihuahuan-Tamaulipan
Parthenium incanum Madrean wide
Pectis angustifolia WC N America
Pectis filipes Sonoran-Chihuahuan
Pectis papposa Madrean (no Mex. Highlands)
Pectis prostrata Mesoam-Central American
Pericome caudata N Madrean
Perityle aglossa Tr-Pecos-Coahuila
Perityle angustifolia SW TX Endemic
Perityle bisetosa Chihuahuan
Perityle cinerea Tr-Pecos Endemic
Perityle dissecta Chihuahuan
Perityle parryi Chihuahuan
Perityle quinqueflora Chihuahuan
Perityle rupestris Chihuahuan
Perityle vaseyi Chihuahuan
Perityle vitreomontana Brewster c Endemic
Pinaropappus roseus Madrean-Mesoam
Pluchea sericea N Madrean
Porophyllum greggii Chihuahuan
Porophyllum ruderale American Trop/Subtr
Porophyllum scoparium Chihuahuan wide
Psathyrotopsis scaposa Chihuahuan
Pseudoclappia arenaria Pecos c. S Rocky M-N Chihuahuan (Coahuila)
Pseudognaphalium arizonicum Sonoran-Chihuahuan
Pseudognaphalium canescens W N American
Pseudognaphalium jaliscense ?
Pseudognaphalium pringlei Sonoran-Chihuahuan

Pseudognaphalium stramineum W N American
Pseudognaphalium viscosum Mesoam
Psilactis asteroides Sonoran-Chihuahuan
Psilactis brevilingulata Chihuahuan (Amphitropical)
Psilostrophe gnaphalioides Chihuahuan-Tamaulipan
Psilostrophe tagetina SWC US
Ratibida columnifera Prairie wide
Ratibida tagetes SWC US
Sanvitalia procumbens Mesoam
Schkuhria multiflora Amphitropical
Senecio flaccidus Madrean wide
Senecio parryi N Sonoran -Chihuahuan
Senecio riddellii W Prairie
Senecio wootonii J Davis, Pecos cc. SWC N American
Simsia calva Chihuahuan-Tamaulipan
Solidago canadensis N American
Solidago gigantea N American
Solidago juliae Chihuahuan
Solidago velutina W N American (not Pacific)
Solidago wrightii S Rocky M-W Madrean
Stephanomeria minor W N American
Stephanomeria pauciflora W N American
Stevia ovata Mesoam-S American
Stevia serrata J Davis c. Mesoam
Symphyotrichum divaricatum ?
Symphyotrichum ericoides N American
Symphyotrichum expansum ?
Symphyotrichum falcatum WC N American (W Prairie wide)
Symphyotrichum lanceolatum J Davis c. N American
Symphyotrichum subulatum American (coastal) Polichorous
Tagetes micrantha Mesoam-Madrean
Tetragonotheca texana Chihuahuan-Tamaulipan
Tetraneuris linearifolia S Prairie-Chihuahuan-Tamaulipan
Tetraneuris scaposa W Prairie-Chihuahuan-Tamaulipan
Thelesperma ambiguum Tamaulipan
Thelesperma filifolium Prairie
Thelesperma longipes Chihuahuan (+ S AZ)
Thelesperma megapotamicum Prairie, secondarily Amphitropical
Thelesperma simplicifolium Chihuahuan (Tamaulipan ?)
Thymophylla acerosa N Madrean wide
Thymophylla aurea ?
Thymophylla micropoides Chihuahuan
Thymophylla pentachaeta Madrean
Thymophylla setifolia Chihuahuan
Townsendia exscapa W N American
Trixis californica N Madrean
Verbesina encelioides Amerrican
Verbesina nana Chihuahuan
Verbesina oreophila Chihuahuan Mont
Verbesina virginica J Davis c. E N American
Vernonia larsenii Chihuahuan
Vernonia marginata W Prairie-Chihuahuan
Viguiera cordifolia N Sonoran-Chihuahuan
Viguiera dentata Mesoam-Madrean
Viguiera stenoloba Madrean (Chihuahuan wide)
Wedelia texana Chihuahuan-Tamaulipan
Xanthocephalum gymnospermoides J Davis c. Sonoran-Chihuahuan
Xylorhiza wrightii Chihuahuan
Xylothamia triantha Chihuahuan
Zinnia acerosa Madrean wide
Zinnia anomala Chihuahuan
Zinnia grandiflora S Rocky M-Sonoran wide

AZOLLACEAE: 1/1
Azolla mexicana C & N American

BERBERIDACEAE: 2/1
Mahonia haematocarpa Sonoran
Mahonia trifoliolata Sonoran

BETULACEAE: 1/1
Ostrya virginiana Appalachian. E N American

BIGNONIACEAE: 2/2
Chilopsis linearis Sonoran wide
Tecoma stans American Trop/Subtr

BORAGINACEAE: 33/9
Amsinckia menziesii W US
Antiphytum floribundum E & S Madrean
Antiphytum heliotropioides S Chihuahuan (Coahuila)
Cryptantha albida Sonoran-Chihuahuan
Cryptantha angustifolia SW N American
Cryptantha cinerea W N American
Cryptantha crassipes Endemic for Otero, NM, & Brewster, TX, cc. N Chihuahuan
Cryptantha crassisepala Sonoran wide
Cryptantha mexicana Chihuahuan
Cryptantha oblata Endemic S NM – SW TX
Cryptantha palmeri Chihuahuan
Cryptantha pusilla Sonoran-Chihuahuan
Hackelia pinetorum SW US (AZ, NM, SW TX)
Heliotropium confertifolium Chihuahuan
Heliotropium convolvulaceum WC N American
Heliotropium curassavicum American
Heliotropium glabriusculum Chihuahuan
Heliotropium greggii Chihuahuan
Heliotropium molle Chihuahuan
Heliotropium procumbens Caribbean with irradiations to N & S America. American
Heliotropium torreyi Chihuahuan-Tamaulipan
Lappula occidentalis W N American
Lithospermum cobrense Apachian-SMO
Lithospermum incisum W US-Prairie wide
Lithospermum mirabile S TX Endemic
Lithospermum multiflorum S WC US
Lithospermum viride Chihuahuan rare
Omphalodes aliena Chihuahuan narrow
Tiquilia canescens Madrean
Tiquilia gossypina Chihuahuan
Tiquilia greggii Chihuahuan
Tiquilia hispidissima Chihuahuan
Tiquilia mexicana Chihuahuan

BRASSICACEAE: 43/21
Arabis fendleri W N American (Great Basin-S Rocky M)
Cardamine macrocarpa Chihuahuan, rare

Descurainia incana J Davis c. W N American
Descurainia pinnata N American (mostly W)
Dimorphocarpa wislizeni N Sonoran–S Rocky M
Draba cuneifolia W & SC N American
Draba platycarpa W & SC US disjunct
Draba standleyi Apachian ? Rare
Erysimum asperum Prairie (mostly W)
Erysimum capitatum W N American
Halimolobos diffusa Sonoran Mont
Lepidium alyssoides S Rocky M-E Great Basin
Lepidium austrinum SC N American
Lepidium densiflorum N American
Lepidium lasiocarpum Great Basin-Sonoran
Lepidium oblongum S & C N American
Lepidium sordidum Chihuahuan
Lepidium virginicum N American
Lesquerella argyraea Chihuahuan
Lesquerella fendleri S Rocky M-(SE Great Basin)-Sonoran
Lesquerella gordonii Sonoran-SE Prairie
Lesquerella mcvaughiana Brewster & Pecos cc Endemic
Lesquerella ovalifolia C Prairie-N Sonoran
Lesquerella purpurea N Sonoran proper
Mancoa pubens N Sonoran-Chihuahuan disjunct
Nerisyrenia camporum Chihuahuan proper
Noccaea montana W US Mont not Cal Province
Pennellia longifolia J Davis c. S Great Basin-Sonoran
Pennellia micrantha S Great Basin-Sonoran
Rorippa ramosa Chihuahuan rare
Rorippa teres Gulf Coast
Schoenocrambe linearifolia W N American
Selenia dissecta N Sonoran-Chihuahuan disjunct
Sisymbrium auriculatum Chihuahuan
Stanleya pinnata W N American
Streptanthus carinatus N (Sonoran) Chihuahuan
Streptanthus cutleri Brewster c. Endemic
Streptanthus platycarpus SW TX Endemic
Synthlipsis greggii Chihuahuan
Thelypodiopsis purpusii SW US (?)
Thelypodium tenue Tr-Pecos Endemic
Thelypodium texanum Tr-Pecos Endemic
Thelypodium wrightii SW US (Apachian ?)

BROMELIACEAE: 2/2
Hechtia texensis Tr-Pecos Endemic (Big Bend)
Tillandsia recurvata American Trop/Subtr

BUDDLEJACEAE: 3/2
Buddleja marrubiifolia Chihuahuan
Buddleja scordioides E Madrean
Emorya suaveolens Tr-Pecos-Coahuila

CACTACEAE: 56/17
Ariocarpus fissuratus Chihuahuan
Coryphantha echinus Chihuahuan
Coryphantha macromeris Chihuahuan
Coryphantha ramillosa Chihuahuan (Coahuila)
Coryphantha robustispina Sonoran-Chihuahuan
Cylindropuntia davisii Chihuahuan+ SWC US
Cylindropuntia imbricata S N American
Cylindropuntia kleiniae Sonoran-Chihuahuan
Cylindropuntia leptocaulis Chihuahuan-Tamaulipan
Cylindropuntia tunicata Madrean + Ecuador, Peru
Echinocactus horizonthalonius Chihuahuan
Echinocactus texensis Chihuahuan-Tamaulipan+ SWC US
Echinocereus chisoensis ?
Echinocereus coccineus SW US-Sonoran wide (no Cal)
Echinocereus dasyacanthus Chihuahuan
Echinocereus enneacanthus Chihuahuan-Tamaulipan
Echinocereus pectinatus Chihuahuan-Tamaulipan
Echinocereus pseudopectinatus ?
Echinocereus russanthus Brewster c. Endemic
Echinocereus stramineus Chihuahuan
Echinocereus viridiflorus W Prairie-Chihuahuan
Echinomastus intertextus Sonoran-Chihuahuan
Echinomastus mariposensis Chihuahuan
Echinomastus warnockii Chihuahuan
Epithelantha micromeris Sonoran-Chihuahuan
Escobaria albicolumnaria Chihuahuan
Escobaria dasyacantha Chihuahuan
Escobaria duncanii Chihuahuan
Escobaria hesteri Tr-Pecos Endemic
Escobaria minima Brewster c. Endemic
Escobaria tuberculosa Chihuahuan
Escobaria vivipara W N American
Ferocactus hamatacanthus Chihuahuan-Tamaulipan
Glandulicactus uncinatus var. *wrightii* Chihuahuan
Grusonia aggeria Tr-Pecos-Coahuila
Grusonia emoryi Chihuahuan
Grusonia grahamii Tr-Pecos
Grusonia schottii Chihuahuan-Tamaulipan
Lophophora williamsii Chihuahuan-Tamaulipan
Mammillaria grahamii Sonoran-Chihuahuan
Mammillaria heyderi Sonoran wide (+Tamauilipas)
Mammillaria heyderi var. *meiacantha* Apachian
Mammillaria lasiacantha Sonoran-Chihuahuan
Mammillaria pottsii Chihuahuan
Neolloydia conoidea Chihuahuan-Tamaulipan
Opuntia atrispina S TX Endemic
Opuntia aureispina Brewser c. Endemic
Opuntia engelmannii Sonoran wide
Opuntia engelmannii var. *lindheimeri* SC N American (Chihuahuan-Tamaulipan)
Opuntia macrocentra Sonoran wide
Opuntia macrorhiza C N American
Opuntia phaeacantha SW N American
Opuntia polyacantha W N American
Opuntia rufida Chihuahuan
Peniocereus greggii Sonoran wide
Thelocactus bicolor Chihuahuan-Tamaulipan

CALLITRICHACEAE:1/1
Callitriche heterophylla J Davis c. C&N American

CAMPANULACEAE: 6/3
Campanula rotundifolia Holarctical (Palearctical)
Lobelia berlandieri Chihuahuan
Lobelia cardinalis N American
Lobelia fenestralis Tr-Pecos, AZ, Mexico, SW NM Disjunct Mont

Triodanis holzingeri CS Prairie
Triodanis perfoliata N American

CAPPARACEAE: 6/5
Cleome multicaulis Disjunct: AZ. CO. TX, WO. S Rocky M-W Madrean
Cleomella longipes Sonoran-Chihuahuan (W)
Koeberlinia spinosa Amphitropical (NW Sonoran-Chihuahuan)
Polanisia dodecandra N American
Polanisia uniglandulosa Madrean (Mexican Highlands–N&E Madrean)
Wislizenia refracta Sonoran

CAPRIFOLIACEAE: 5/3
Lonicera albiflora SWC US disjunct mont
Symphoricarpos longiflorus N Madrean
Symphoricarpos palmerii N Madrean
Viburnum australe J Davis c, rare, also in Mexico ?
Viburnum rufidulum J Davis c. E N American

CARYOPHYLLACEAE: 15/5
Arenaria benthamii SC US. C-S Texas
Arenaria fendleri J Davis c. S Rocky M-S Great Basin-Apachian
Arenaria lanuginosa Davis c. N American ?
Arenaria livermorensis J Davis c. Tr-Pecos Endemic
Arenaria ludens Tr-Pecos-Coahuila
Cerastium axillare Chihuahuan
Drymaria laxiflora Chihuahuan
Drymaria leptophylla SWC N American (Sonoran ?)
Drymaria molluginea J Davis c. SWC N American
Drymaria pachyphylla N Chihuahuan
Paronychia jamesii SC US
Paronychia monticola Tr-Pecos –Coahuila Mont
Paronychia wilkinsonii Chihuahuan Mont
Silene antirrhina N American
Silene laciniata Madrean wide

CELASTRACEAE: 4/3
Celastrus scandens N American (NE-NC)
Mortonia sempervirens Chihuahuan
Mortonia scabrella N Sonoran- Chihuahuan
Schaefferia cuneifolia Chihuahuan

CERATOPHYLLACEAE: 1/1
Ceratophyllum demersum Polychorous

CHENOPODIACEAE: 21/6
Atriplex acanthocarpa Chihuahuan
Atriplex canescens W US (+ Chihuahua)
Atriplex elegans N Madrean
Atriplex obovata SE Great Basin-S Rocky M-Chihuahuan
Atriplex wrightii SW-C US + N Mexico
Chenopodium berlandieri N American
Chenopodium cycloides E CS Prairie
Chenopodium fremontii W N American
Chenopodium incanum W N American
Chenopodium graveolens Amphitropical
Chenopodium leptophyllum W N American
Chenopodium neomexicanum SW US
Chenopodium murale Polichorous (Palearctic)
Chenopodium pallescens Presidio c. ?
Chenopodium pratericola N American
Corispermum americanum WC N American
Cycloloma atriplicifolium N American
Kraschenínnikovia lanata W N American
Monolepis nuttalliana W N American
Suaeda suffrutescens var. *suffrutescens* Apachian-Chihuahuan (+ OK)

CISTACEAE: 2/2
Helianthemum glomeratum C American
Lechea mensalis Chisos Mont. Brewster c Endemic

COMMELINACEAE: 6/2
Commelina dianthifolia S Rocky M- Madrean
Commelina erecta E N American
Tradescantia brevifolia Tr-Pecos-Coahuila Mont
Tradescantia leiandra Chihuahuan
Tradescantia occidentalis Prairie wide
Tradescantia wrightii N Chihuahuan

CONVOLVULACEAE: 16/6
Bonamia ovaliifolia N Chihuahuan
Bonamia repens N Chihuahuan
Convolvulus equitans SWC N American
Cressa truxillensis Madrean
Dichondra argentea Chihuahuan
Dichondra brachypoda Chihuahuan
Evolvulus alsinoides Madrean
Evolvulus nuttallianus WC N American
Evolvulus sericeus J Davis c. American Trop/Subtr
Ipomoea capillacea C American
Ipomoea cardiophylla American Trop/Subtr
Ipomoea costellata Sonoran
Ipomoea cristulata Sonoran
Ipomoea lindheimeri Chihuahuan
Ipomoea rupicola N Chihuahuan
Ipomoea tenuiloba Sonoran

CRASSULACEAE: 6/3
Echeveria strictiflora Chihuahuan
Sedum cockerellii J Davis c. AZ+NM
Sedum havardii Tr-Pecos-Coahuila
Sedum nanifolium Pecos-Coahuila Endemic
Sedum wrightii SWC N American
Villadia squamulosa Chihuahuan

CROSSOSOMATACEAE: 1/1
Glossopetalon spinescens W N American

CUCURBITACEAE: 8/6
Apodanthera undulata Sonoran-Chihuahuan
Cucurbita digitata Madrean
Cucurbita foetidissima Madrean wide (radiations to WC US)
Cyclanthera dissecta Mesoam-Madrean
Ibervillea lindheimeri Comanchian-Caribbean ?
Ibervillea tenuisecta Chihuahuan
Melothria pendula E N American (Gulf Coast)
Sicyos microphyllus Mesoam

CUPRESSACEAE: 8/2
Cupressus arizonica Madrean wide disjunct

Juniperus ashei Comanchian
Juniperus coahuilensis Sonoran-Chihuahuan (wide)
Juniperus deppeana Madrean
Juniperus flaccida Brewster c. only in US. Madrean
Juniperus monosperma Madrean
Juniperus pinchotii SC US
Juniperus scopulorum W N American

CUSCUTACEAE: 6/1
Cuscuta applanata ?
Cuscuta indecora N American
Cuscuta leptantha ?
Cuscuta pentagona American
Cuscuta squamata Chihuahuan
Cuscuta umbellata ?

CYPERACEAE: 40/10
Bulbostylis capillaris American (Amphipacific)
Bulbostylis juncoides S Mesoam
Carex agrostoides Sonoran-Chihuahuan (N)
Carex athrostachya J Davis c. W N American
Carex frankii E N American
Carex hystericina Presidio c N American
Carex mesochorea E N American
Carex microdonta CS Prairie
Carex muriculata Pecos c. Chihuahuan
Carex occidentalis J Davis c. W N American
Carex planostachys SC US-E Madrean + Florida
Cladium mariscus Trop/Subtr
Cyperus acuminatus J Davis, Presidio cc. N American
Cyperus echinatus E N American
Cyperus elegans Mesoam-S American
Cyperus esculentus American-African (Polichorous)
Cyperus flavicomus J Davis c ?
Cyperus laevigatus Trop/Subtr
Cyperus niger American (Trop/Subtr)
Cyperus odoratus American
Cyperus pseudothyrsiflorus SC US (TX, N Mexico)
Cyperus retroflexus S N American
Cyperus seslerioides American (Trop/Subtr)
Cyperus spectabilis Madrean wide
Cyperus sphaerolepis Madrean
Cyperus squarrosus American-African
Eleocharis albida Atlantic-Gulf Coast
Eleocharis cylindrica Presidio c. Amphitropical
Eleocharis geniculata American-African
Eleocharis macrostachya American
Eleocharis montevidensis American
Eleocharis parishii Presidio c Madrean wide
Eleocharis parvula Holarctical
Fimbristylis annua American
Fuirena simplex N American-Mesoam
Lipocarpha aristulata N American
Lipocarpha micrantha American
Schoenoplectus acutus J Davis c. N American
Schoenoplectus maritimus Holarctical
Schoenoplectus pungens Polichorous

DENNSTAEDTIACEAE: 1/1
Pteridium aquilinum Holarctical

DRYOPTERIDACEAE: 4/2
Phanerophlebia umbonata Tamaulipan-Chihuahuan
Woodsia neomexicana Apachian
Woodsia phillipsii Sonoran Subprovince
Woodsia plummerae Sonoran-N Chihuahuan

EBENACEAE: 1/1
Diospyros texana Chihuahuan proper

EPHEDRACEAE: 4/1
Ephedra antisyphilitica Chihuahuan (+NE TX to OK)
Ephedra aspera Madrean disjunct
Ephedra torreyana SW N American
Ephedra trifurca N Madrean

EQUISETACEAE: 3/1
Equisetum arvense Holarctical
Equisetum hyemale Holarctical
Equisetum laevigatum N American

ERICACEAE: 1/1
Arbutus xalapensis Mesoam

EUPHORBIACEAE: 59/10
Acalypha monostachya Chuhuahuan
Acalypha neomexicana Sonoran
Acalypha ostryifolia American (C&N American)
Acalypha phleoides Madrean wide
Andrachne arida Tr-Pecos-Coahuila
Argythamnia humilis S Prarie
Argythamnia neomexicana N Madrean
Bernardia obovata Chuhuahuan
Chamaesyce acuta N Chuhuahuan
Chamaesyce albomarginata N Madrean
Chamaesyce angusta S TX Endemic
Chamaesyce arizonica N Madrean (Sonoran)
Chamaesyce capitellata Sonoran Subprovince
Chamaesyce chaetocalyx Apachian
Chamaesyce cinerascens Chihuahuan-Tamaulipan
Chamaesyce dioica American Trop/Subtr
Chamaesyce fendleri WC US
Chamaesyce geyeri Prairie
Chamaesyce glyptosperma N American
Chamaesyce golondrina SW Texas Endemic
Chamaesyce hyssopifolia American Trop/Subtr
Chamaesyce jejuna N Chihuahuan
Chamaesyce lata SWC US
Chamaesyce micromera N Madrean
Chamaesyce missurica Prairie
Chamaesyce nutans C&N American
Chamaesyce perennans SW Texas Endemic
Chamaesyce prostrata C&N American
Chamaesyce revoluta N Madrean
Chamaesyce serpens American
Chamaesyce serpyllifolia N American with radiations
Chamaesyce serrula Sonoran-Chihuahuan
Chamaesyce setiloba N Madrean
Chamaesyce stictospora C&N American
Chamaesyce theriaca Chihuahuan
Chamaesyce villifera Mesoam-Madrean
Croton dioicus Mexican-Chihuahuan

Croton fruticulosus Chihuahuan-Tamaulipan
Croton incanus E Madrean (Tamaulipan)
Croton lindheimerianus S Prairie
Croton monanthogynus E N American (E Prairie-Gulf Coast)
Croton pottsii Sonoran-Chihuahuan
Croton sancti-lazari Chihuahuan
Euphorbia antisyphilitica Madrean
Euphorbia bifurcata E Madrean
Euphorbia brachycera W N American
Euphorbia cyathophora N American
Euphorbia davidii N American
Euphorbia dentata N American
Euphorbia eriantha N Madrean, disjunct
Euphorbia exstipulata N Madrean
Euphorbia marginata American
Euphorbia radians Madrean
Euphorbia spathulata N American
Jatropha dioica (only TX in US) Madrean
Phyllanthus ericoides N Chihuahuan
Phyllanthus polygonoides SC N American
Tragia amblyodonta Sonoran wide
Tragia ramosa: SWC US

FABACEAE: 107/37

Acacia angustissima American Trop/Subtr
Acacia berlandieri Chihuahuan
Acacia constricta Madrean wide
Acacia farnesiana Pantropical
Acacia greggii Madrean
Acacia neovernicosa Sonoran
Acacia rigidula Chihuahuan-Tamaulipan
Acacia roemeriana Chihuahuan
Acacia schottii (Brewster & Presidio cc) N Chihuahuan
Amorpha fruticosa Presidio c. N American
Astragalus crassicarpus Prairie wide
Astragalus emoryanus S Great Basin-N Chihuahuan disjunct
Astragalus giganteus N Chihuahuan
Astragalus humistratus S Great Basin-N Sonora-Chihuahuan
Astragalus lotiflorus Prairie
Astragalus missouriensi S Rocky M-Prairie
Astragalus mollissimus WC N American
Astragalus nuttallianus WC N American
Astragalus nuttallianus var. *austrinus* SWC N American
Astragalus wrightii S TX Endemic
Brongniartia minutifolia Tr-Pecos Endemic
Calliandra conferta Madrean (S, C&E)
Calliandra humilis Sonoran
Calliandra iselyi Tr-Pecos Endemic
Cercis canadensis E N American
Chamaecrista nictitans American
Cologania angustifolia Madrean
Cologania pallida Amphitropical ?
Crotalaria pumila American Trop/Subtr
Dalea aurea Prairie
Dalea bartonii Tr-Pecos Endemic
Dalea bicolor Sonoran
Dalea candida Prairie
Dalea enneandra Prairie
Dalea formosa SWC N American
Dalea frutescens E Madrean
Dalea greggii E Madrean
Dalea jamesii Apachian
Dalea lachnostachys N Sonoran-Chihuahuan
Dalea lanata SWC US
Dalea laniceps N Chihuahuan
Dalea leporina American, mostly Mesoam
Dalea nana Sonoran wide
Dalea neomexicana N Sonoran-Chihuahuan
Dalea neomexicana var. *longipila* S Chihuauan-Tamaulipan
Dalea pogonathera Sonoran
Dalea wrightii Sonoran-Chihuahuan
Desmanthus cooleyi Apachian
Desmanthus glandulosus N Sonoran-Chihuahuan
Desmanthus illinoensis Prairie
Desmanthus obtusus N Chihuahuan
Desmanthus velutinus N Chihuahuan
Desmanthus virgatus American (except N)
Desmodium grahamii Madrean
Desmodium neomexicanum Mesoam-Madrean (Amphitropical)
Desmodium psilophyllum Mesoam-E Madrean
Eysenhardtia spinosa Presidio c. Chihuahuan ?
Eysenhardtia texana Chihuahuan
Galactia canescens J Davis c. Chihuahuan
Galactia wrightii Sonoran
Genistidium dumosum Chihuahuan local
Glycyrrhiza lepidota WC N American
Hoffmannseggia drepanocarpa SW US
Hoffmannseggia glauca Amphitropical
Hoffmannseggia oxycarpa Chihuahuan
Indigofera lindheimeriana Chihuahuan
Indigofera miniata Mesoam (Caribbean)
Lespedeza texana Comanchian
Leucaena retusa Chihuahuan
Lotus plebeius SW N American Mont
Lupinus concinnus N Madrean
Lupinus havardii SW TX, N Tamaulipan, MO ?
Lupinus texensis Comanchian
Macroptilium atropurpureum Mesoam
Macroptilium gibbosifolium Mesoam
Mimosa aculeaticarpa Madrean wide
Mimosa borealis SWC US
Mimosa dysocarpa Sonoran wide
Mimosa emoryana Chihuahuan-Mexican Highlands disjunct
Mimosa texana Chihuahuan ?
Mimosa turneri Chihuahuan disjunct ?
Nissolia platycalyx Chihuahuan disjunct, local
Parkinsonia aculeata Subtropical
Peteria scoparia Apachian ?
Phaseolus filiformis Sonoran Subprovince
Pomaria jamesii SWC US wide
Pomaria melanosticta Tr-Pecos-Coahuila
Prosopis glandulosa W N American (mostly S)
Prosopis pubescens N Madrean
Psoralidium tenuiflorum Prairie-SWC US
Rhynchosia senna Amphitropical
Senna alata Trop/Subtr

Senna bauhinioides Madrean
Senna durangensis Chihuahuan-Tamaulipan disjunct local ?
Senna lindheimeriana Chihuahuan-Tamaulipan
Senna orcuttii Sonoran-Chihuahuan local
Senna pilosior Chihuahuan
Senna pumilio (S Prairie-Chihuahuan) SC N American
Senna roemeriana (NM & W TX) SWC US
Senna ripleyana Brewster c. ?
Senna wislizeni N & E Madrean (disjunct)
Sesbania herbacea Mesoam
Sophora nuttalliana WC N America
Sophora secundiflora E Madrean
Tephrosia vicioides Mesoam
Vicia americana N American (mostly W & N)
Vicia ludoviciana N American (S)

FAGACEAE: 20/1
Quercus arizonica Sonoran-Chihuahuan
Quercus carmenensis Chihuahuan local
Quercus depressipes J Davis c. Chihuahuan local
Quercus emoryi Sonoran-Chihuahuan
Quercus gambelii W N American
Quercus graciliformis Brewster c. Endemic
Quercus gravesii Chihuahuan
Quercus grisea Sonoran wide
Quercus hinckleyi Presidio Endemic
Quercus hypoleucoides Sonoran-Chihuahuan
Quercus intricata Chihuahuan
Quercus laceyi E Madrean
Quercus mohriana SWC US
Quercus muehlenbergii E N American
Quercus oblongifolia W Madrean
Quercus pungens Madrean (E)
Quercus robusta Brewster c. Endemic
Quercus rugosa Mesoam-Madrean
Quercus tardifolia Brewster c. Endemic
Quercus turbinella SW N American
Quercus vaseyana Chihuahuan

FOUQUIERIACEAE: 1/1
Fouquieria splendens Sonoran-Chihuahuan (N&W Madrean)

FUMARIACEAE: 2/1
Corydalis aurea Prairie N American (WC)
Corydalis curvisiliqua Prairie N American (C-SW)

GARRYACEAE: 2/1
Garrya ovata S&E Madrean
Garrya wrightii Sonoran

GENTIANACEAE: 6/3
Centaurium arizonicum N Madrean
Centaurium beyrichii Comanchian (SC US ?)
Centaurium calycosum E Madrean
Centaurium glanduliferum Tr-Pecos Endemic
Eustoma exaltatum Mesoam-N American
Gentiana affinis W N American

GERANIACEAE: 3/2
Erodium texanum SWC US ?
Geranium caespitosum W N American
Geranium carolinianum J Davis c. American

GROSSULARIACEAE: 3/1
Ribes aureum N American (not E & SE)
Ribes leptanthum J Davis c. SW N American (US)
Ribes mescalerium SWC US (SW TX-SC NM)

HYDRANGEACEAE: 8/2
Fendlera rigida Tr-Pecos-Coahuila
Fendlera rupicola Apachian
Fendlera wrightii ?
Fendlerella utahensis SW US
Philadelphus crinitus J Davis c. Endemic ?
Philadelphus mearnsii Amphitropical ? (SW US)
Philadelphus microphyllus SW US wide
Philadelphus serpyllifolius SW US disjunct

HYDROPHYLLACEAE: 15/2
Nama dichotomum W American
Nama havardii N Chihuahuan
Nama hispidum SWC N American
Nama parvifolium Chihuahuan-Tamaulipan
Nama torynophyllum Chihuahuan
Nama undulatum Chihuahuan-Tamaulipan
Phacelia caerulea Sonoran Subprovince
Phacelia congesta SC N American
Phacelia crenulata SW US
Phacelia infundibuliformis Tr-Pecos
Phacelia integrifolia SWC US
Phacelia pallida Tr-Pecos, rare
Phacelia popei SWC US
Phacelia robusta Tr-Pecos-Coahuila
Phacelia rupestris N Sonoran-Chihuahuan

IRIDACEAE: 2/1
Sisyrinchium (demissum) ?
Sisyrinchium cernuum J Davis c. W Madrean

JUGLANDACEAE: 3/2
Carya illinoinensis J Davis c. E N American
Juglans major Madrean wide
Juglans microcarpa SC N American

JUNCACEAE: 8/1
Juncus acuminatus N American-C American
Juncus arcticus J Davis c. Polichorous (Arcto-Mont)
Juncus bufonius Polichorous
Juncus ensifolius W N American
Juncus interior Prairie wide
Juncus marginatus J Davis c. American
Juncus nodosus N American
Juncus torreyi N American

KRAMERIACEAE: 3/1
Krameria erecta Sonoran (mostly W)
Krameria grayi Sonoran
Krameria lanceolata SC N American (+ Florida)

LAMIACEAE: 38/11
Agastache micrantha Chihuahuan (mostly W)
Agastache pallidiflora Sonoran
Hedeoma costata E Madrean-Caribbean
Hedeoma drummondii WC N American
Hedeoma mollis Tr-Pecos Endemic

Hedeoma nana N Madrean
Hedeoma pilosa (Extinct)
Hedeoma plicata N Chihuahuan
Hedeoma reverchonii Comanchian (TX, S OK)
Hedeoma reverchonii var. *serpyllifolia* ? S TX
Mentha arvensis Holarctical
Monarda citriodora Prairie-SWC US
Monarda fistulosa J Davis c. N American
Monarda pectinata WC US
Physostegia virginiana J Davis c. E N American
Poliomintha glabrescens Chihuahuan
Salazaria mexicana N Madrean (mostly Mohavean)
Salvia arizonica Sonoran -Chihuahuan disjunct
Salvia azurea EC US
Salvia farinacea SC US (S Prairie)
Salvia greggii Chihuahuan-Tamaulipan
Salvia henryi Sonoran- Chihuahuan (W)
Salvia lycioides Chihuahuan
Salvia reflexa N American (mostly Prairie)
Salvia regla Madrean
Salvia roemeriana Chihuahuan proper
Salvia texana Pecos c. SC N American
Salvia tiliifolia Mesoam-S American (NW)
Salvia whitehousei N Chihuahuan
Scutellaria drummondii SC-SE N American
Scutellaria potosina Sonoran-Chihuahuan
Scutellaria texana Chihuahuan
Scutellaria wrightii SC N American (TX-OK)
Stachys bigelovii Chihuahuan
Teucrium canadense J Davis c. N American-Mesoam
Teucrium coahuilanum Tr-Pecos-Coahuila
Teucrium cubense Mesoam-Madrean
Teucrium laciniatum SWC US

LEMNACEAE: 3/2
Lemna minuta J Davis c. American
Lemna valdiviana American
Spirodela polyrrhiza J Davis c. American

LILIACEAE: 16/8
Allium cernuum N American
Allium glandulosum Sonoran-Mexican Highlands
Allium kunthii Madrean
Allium coryi SW TX Endemic
Allium drummondii SC US (Prairie)
Allium perdulce Prairie
Cooperia drummondii Pecos c. SC US (+NE Mexico)
Dasylirion leiophyllum Chihuahuan
Dasylirion texanum Chihuahuan-Tmaulipan
Echeandia flavescens J Davis c. Sonoran (W)
Maianthemum racemosum J Davis c. N American Mont
Nolina erumpens Chihuahuan
Nolina texana SWC US
Nothoscordum bivalve E N American-Mesoam
Schoenocaulon texanum Chihuahuan
Zephyranthes longifolia N Sonoran-Chihuahuan

LINACEAE: 8/1
Linum aristatum SW N American
Linum berlandieri Prairie (SC)
Linum hudsonioides S Prairie
Linum lewisii W N American
Linum puberulum W N American
Linum rupestre Madrean wide
Linum schiedeanum E Madrean-Mesoam
Linum vernale Chihuahuan

LOASACEAE: 11/3
Cevallia sinuata Sonoran wide
Eucnide bartonioides Chihuahuan-Tamaulipan
Mentzelia albescens Amphitropical
Mentzelia asperula N Sonoran disjunct
Mentzelia lindheimeri Chihuahuan-Tamaulipan
Mentzelia mexicana Chihuahuan
Mentzelia multiflora Madrean (N)-S Rocky M
Mentzelia oligosperma Prairie
Mentzelia pachyrhiza Chihuahuan
Mentzelia reverchonii SC US
Mentzelia saxicola Presidio c. Chihuahuan

LYTHRACEAE: 2/2
Lythrum californicum W N American
Nesaea longipes N Chihuahun

MALPIGHIACEAE: 1/1
Janusia gracilis Sonoran (+W Chihuahuan)

MALVACEAE: 24/12
Abutilon fruticosum Tropical
Abutilon malacum Sonoran
Abutilon parvulum Sonoran
Abutilon wrightii Chihuahuan
Allowissadula holosericea Chihuahuan-Tamaulipan
Batesimalva violacea Chihuahuan-Tamaulipan
Callirhoe involucrata Prairie
Herissantia crispa Trop/Subtr
Hibiscus coulteri Sonoran wide
Hibiscus denudatus S California-Sonoran
Malvella lepidota Sonoran
Malvella leprosa Amphitropical ?
Malvella sagittifolia Sonoran
Meximalva filipes Tamaulipan
Modiola caroliniana American Trop/Subtr
Rhynchosida physocalyx S American
Sida longipes Chihuahuan-Tamaulipan
Sida neomexicana Sonoran-Chihuahuan ?
Sphaeralcea angustifolia Madrean
Sphaeralcea coccinea W N American
Sphaeralcea digitata S Great Basin-Chihuahuan
Sphaeralcea hastulata S Great Basin-S Rocky M-Sonoran wide
Sphaeralcea incana S Great Basin-S Rocky M-Chihuahuan
Sphaeralcea leptophylla S Great Basin-S Rocky M-N Chihuahuan

MARSILEACEAE: 2/1
Marsilea mollis Mesoam-S American
Marsilea vestita N American (+ Peru)

MENISPERMACEAE: 1/1
Cocculus carolinus E N American

MOLLUGINACEAE: 1/1
Mollugo verticillata American (Trop/Subtr)

MORACEAE: 2/1
Morus microphylla S Great Basin-Sonoran-N Chihuahuan

NAJADACEAE: 1/1
Najas guadalupensis American

NYCTAGINACEAE: 32/11
Abronia angustifolia S Great Basin-Sonoran
Acleisanthes acutifolia Chihuahuan
Acleisanthes longiflora Sonoran wide
Acleisanthes wrightii SW TX Endemic
Allionia choisyi Amphitropical ?
Allionia incarnata American (SW N, C, S)
Ammocodon chenopodioides Sonoran
Anulocaulis eriosolenus Chihuahuan
Anulocaulis leiosolenus SW N American
Anulocaulis reflexus N Chihuahuan local
Boerhavia anisophylla Madrean
Boerhavia coccinea Trop/Subtr
Boerhavia erecta American Trop/Subtr
Boerhavia gracillima Sonoran wide
Boerhavia intermedia Sonoran wide (N&W Madrean)
Boerhavia linearifolia Chihuahuan (+N NM)
Boerhavia torreyana Apachian
Boerhavia spicata Sonoran (W)
Boerhavia wrightii N Madrean
Commicarpus scandens American Trop/Subtr
Cyphomeris crassifolia E Chihuahuan
Cyphomeris gypsophiloides Chihuahuan wide
Mirabilis albida N American (Prairie-SW N American)
Mirabilis linearis W N American (+Prairie)
Mirabilis longiflora Sonoran wide
Mirabilis multiflora SW N American
Mirabilis oxybaphoides SW N American
Mirabilis texensis SW TX
Nyctaginia capitata Chihuahuan
Selinocarpus angustifolius Chihuahuan
Selinocarpus diffusus Pecos c. SWC US (W TX-NM)
Selinocarpus parvifolius Tr-Pecos Endemic

OLEACEAE: 8/3
Forestiera angustifolia Chihuahuan-Tamaulipan
Fraxinus cuspidata N & E Madrean Mont
Fraxinus greggii E Madrean Mont
Fraxinus papillosa N Sonoran-Chihuahuan
Fraxinus velutina N&W Madrean Mont
Menodora heterophylla N Chihuahuan (S TX)
Menodora longiflora N Chihuahuan (S TX)
Menodora scabra Madrean (no Mexican Highlands)

ONAGRACEAE: 28/4
Camissonia chamaenerioides N Madrean
Epilobium ciliatum W American
Ludwigia palustris Polichorous
Ludwigia peploides American (Polichorous)
Ludwigia repens E N American (with radiations)
Oenothera arida Chihuahuan
Oenothera albicaulis WC US
Oenothera boquillensis Chihuahuan
Oenothera brachycarpa Madrean (no Mexican Highlands)
Oenothera calcicola E Madrean
Oenothera coccinea N American-Mesoam
Oenothera elata subsp. *hirsutissima* W N American
Oenothera engelmannii SWC US ? (E NM-W TX)
Oenothera grandis Prairie
Oenothera hartwegii SWC US
Oenothera havardii Chihuahuan
Oenothera hexandra Mesoam-Madrean
Oenothera kunthiana Mesoam-Madrean
Oenothera lavandulifolius W N American
Oenothera macrocarpa Tr-Pecos
Oenothera pallida W US (not Pacific)
Oenothera primiveris N Madrean
Oenothera rosea Trop/Subtr (mostly American)
Oenothera speciosa N American-Mesoam
Oenothera suffulta subsp. *nealleyi* N Chihuahuan
Oenothera texensis Chihuahuan
Oenothera triloba Prairie
Oenothera tubicula N Chihuahuan

ORCHIDACEAE: 9/4
Dichromanthus cinnabarinus E Madrean
Epipactis gigantea W N American
Hexalectris grandiflora J Davis c. Madrean disjunct
Hexalectris nitida SE NM-S TX rare
Hexalectris revoluta ? (S AZ-SE NM-S TX)
Hexalectris spicata E N American (also S N America)
Hexalectris warnockii ? (S AZ-SW-SC TX)
? *Malaxis erhenbergii* Chisos, Brewster c. Endemic
Malaxis soulei J Davis c. American Trop/Subtr

OROBANCHACEAE: 4/2
Conopholis alpina Madrean-Mesoam (C American)
Orobanche ludoviciana N American (US)
Orobanche multicaulis Mexican Highlands-Chihuahuan ?
Orobanche uniflora J Davis c. N American

OXALIDACEAE: 3/1
Oxalis albicans Madrean wide
Oxalis dillenii N American
Oxalis drummondii Sonoran-Chihuahuan

PAPAVERACEAE: 4/1
Argemone aenea J Davis N Chihuahuan-Tamaulipan
Argemone chisosensis Chihuahuan
Argemone polyanthemos J Davis c. Prairie
Argemone sanguinea E Chihuahuan-Tamaulipan
Argemone squarrosa SWC US

PASSIFLORACEAE: 1/1
Passiflora tenuiloba Tamaulipan-N Chihuahuan

PEDALIACEAE: 4/1
Proboscidea althaeifolia Sonoran
Proboscidea louisianica N American (mostly S US)
Proboscidea parviflora N Madrean
Proboscidea spicata N Chihuahuan (local)

PHYTOLACCACEAE: 2/2
Phytolacca americana N American (mostly E)
Rivina humilis American Trop/Subtr

PINACEAE: 5/2
Pinus cembroides Madrean wide

Pinus ponderosa W N American
Pinus remota Trans-Pecos-Coahuila
Pinus strobiformis J Davis c. Apachian (AZ, NM)
Pseudotsuga menziesii W N American

PLANTAGINACEAE: 7/1
Plantago helleri SC US
Plantago hookeriana SC US (TX + Coahuila)
Plantago ovata S Palearctical/Paleotropical
Plantago rhodosperma Prairie (adventive in SW)
Plantago major Polichorous
Plantago patagonica American
Plantago wrightiana S N American

PLUMBAGINACEAE: 2/2
Limonium limbatum Pecos c. SWC US (Apachian-N Chihuahuan)
Plumbago scandens Trop American

POACEAE: 202/63
Achnatherum aridum N Madrean
Achnatherum curvifolium N Chihuahuan
Achnatherum eminens CS Madrean (proper)
Achnatherum lobatum N Chihuahuan
Agrostis exarata W N American
Agrostis hyemalis N American
Agrostis stolonifera Holarctical (Boreal)
Allolepis texana Tr-Pecos-Coahuila
Andropogon gerardii N American
Andropogon glomeratus Mesoam wide
Aristida adscensionis Polichorous (Trop/Subtr)
Aristida arizonica N Madrean
Aristida desmantha SC US (E TX & Tr-Pecos)
Aristida divaricata Mesoam-Madrean
Aristida havardii Madrean proper
Aristida pansa Madrean proper
Aristida purpurea N American (W-C)
Aristida purpurea var. *nealleyi* SW N American
Aristida purpurea var. *wrightii* SW N American
Aristida schiedeana Mesoam-N S American
Aristida ternipes Mesoam-Madrean-N S American
Blepharidachne bigelovii Tr-Pecos-Coahuila
Blepharoneuron tricholepis S Rocky M-Madrean
Bothriochloa alta Mesoam-Amphitropical Mont
Bothriochloa barbinodis American Trop/Subtr
Bothriochloa laguroides American (subtr)
Bothriochloa springfieldii American (subtr)
Bouteloua aristidoides American (subtr)
Bouteloua barbata American (subtr)
Bouteloua breviseta Chihuahuan
Bouteloua chondrosioides Mesoam-Madrean
Bouteloua curtipendula American
Bouteloua dactyloides Prairie wide (+ Mexico)
Bouteloua eriopoda SWC US (N Madrean)
Bouteloua gracilis WC N American
Bouteloua hirsuta Prairie-N Madrean
Bouteloua kayi Brewster c. Endemic
Bouteloua ramosa N Chihuahuan
Bouteloua simplex J Davis c. American (Warm-Trop/Subtr)
Bouteloua trifida N Madrean
Bouteloua uniflora Chihuahuan
Bouteloua warnockii N Chihuahuan
Bromus anomalus Mesoam-Madrean
Bromus arizonicus J Davis c. California-Sonoran
Bromus ciliatus Holarctical
Bromus lanatipes SW US (Colorado-Apachian)
Bromus marginatus W N American
Bromus polyanthus W N American Mont
Bromus rubens Pecos c. W N American
?*Cathestecum erectum* S AZ-Tr-Pecos-Guatemala ?
Cenchrus longispinus N American
Cenchrus myosuroides AmericanTrop/Subtr
Cenchrus spinifex ?
Chloris cucullata SC N American
Chloris submutica CS Madrean
Chloris texensis SW & SE TX Endemic
Chloris verticillata Prairie (+WN American)
Chloris virgata American-African (Trop/Subtr)
Cottea pappophoroides American (Amphitropical)
Dasyochloa pulchella Madrean wide
Dichanthelium acuminatum N American-Mesoam
Dichanthelium oligosanthes N American
Digitaria californica Amphitropical
Digitaria ciliaris Polichorous (Warm-Trop/Subtr)
Digitaria cognata E N American
Digitaria hitchcockii S TX- Coahuila
Digitaria patens SW-SC TX Endemic
Digitaria pubiflora SWC US-Chihuahuan (+Tamaulipan)
Digitaria sanguinalis Warm/Subtr
Distichlis spicata American
Echinochloa colona Trop/Subtr/Warm
Echinochloa crus-galli Subtr/Warm
Echinochloa crus-pavonis Presidio c. Trop/Subtr/Warm (American-African)
Echinochloa muricata N American
Elionurus barbiculmis Sonoran-Mexican Highlands
Elionurus tripsacoides American Trop/Subtr
Elymus arizonicus Sonoran-Chihuahuan
Elymus canadensis N American
Elymus elymoides W N American
Elymus trachycaulus N American (W&N)
Enneapogon desvauxii Warm/Subtr
Eragrostis barrelieri Warm Temp/Subtr (+ Trop Africa)
Eragrostis cilianensis Polichorous
Eragrostis curtipedicellata SC US
Eragrostis erosa J Davis, Presidio cc. N Chihuahuan
Eragrostis intermedia SW-SC US-Madrean
Eragrostis lehmanniana Sonoran wide
Eragrostis lugens American Trop/Subtr
Eragrostis mexicana W American
Eragrostis palmeri Chihuahuan wide
Eragrostis pectinacea American
Eriochloa acuminata ?
Erioneuron avenaceum Amphitropical
Erioneuron nealleyi Chihuahuan
Erioneuron pilosum WC N American
Festuca arizonica SW US
Festuca ligulata Chihuahuan
Festuca rubra Holarctical

Hesperostipa neomexicana SW US
Heteropogon contortus Trop/Subtr
Hilaria belangeri Chihuahuan wide
Hilaria swallenii N Chihuahuan
Hordeum jubatum Holarctical
Hordeum pusillum N American
Imperata brevifolia N&W Madrean
Koeleria macrantha Holarctical
Leersia oryzoides Holarctical
Leptochloa dubia American Warm/Subtr
Leptochloa fusca Polichorous
Leptochloa panicea Trop/Subtr (America-Asia)
Lycurus phleoides American Trop/Subtr
Lycurus setosus Amphitropical
Melica montezumae Chihuahuan
Melica nitens Appalachian (E N American)
Melica porteri SW US (Colorado-Apachian)
Microchloa kunthii Trop/Subtr (American-African)
Monroa squarrosa WC US
Muhlenbergia arenacea N Sonoran-Chihuahuan
Muhlenbergia arenicola SWC US-Chihuahuan
Muhlenbergia asperifolia W American (N Temp)
Muhlenbergia brevis SWC US-Chihuahuan
Muhlenbergia depauperata W Madrean Mont
Muhlenbergia dubia Madrean Mont
Muhlenbergia eludens Sonoran-Chihuahuam Mont
Muhlenbergia emersleyi Madrean wide
Muhlenbergia fragilis Madrean Mont (mostly W)
Muhlenbergia glauca Madrean
Muhlenbergia minutissima W N American
Muhlenbergia montana W N American
Muhlenbergia pauciflora SW US-W Madrean Mont
Muhlenbergia polycaulis W Madrean Mont
Muhlenbergia porteri N&WC Madrean
Muhlenbergia repens Madrean
Muhlenbergia rigens NC Madrean
Muhlenbergia rigida W American Mont
Muhlenbergia schreberi E N American (+S America)
Muhlenbergia setifolia Chihuahuan
Muhlenbergia spiciformis ? Caribbean
Muhlenbergia tenuifolia Madrean
Muhlenbergia texana W Madrean
Muhlenbergia torreyi SW US
Muhlenbergia villiflora Chihuahuan Mont
Nassella leucotricha S Prairie-E&S Madrean
Nassella tenuissima Amphitropical (E Madrean)
Panicum bulbosum American
Panicum capillare N American (+Temp S America)
Panicum hallii SWC US
Panicum hirticaule American (Warm/Trop/Subtr)
Panicum obtusum SWC N America
Panicum virgatum N American wide
Pappophorum bicolor Chihuahuan-Mexican Highlands
Pappophorum vaginatum Amphitropical
Pascopyrum smithii W US
Paspalum distichum Warm Temperate/Trop/Subtr
Paspalum pubiflorum E N American-Mesoam
Phalaris angusta American (coastal)
Phalaris caroliniana N American (coastal)
Phragmites australis Polichorous (warm)
Piptochaetium fimbriatum Madrean wide
Piptochaetium pringlei J Davis c. W Sonoran
Pleuraphis jamesii Presidio c. SW US
Pleuraphis mutica Sonoran wide
Poa arachnifera S Prairie
Poa bigelovii N Madrean (SWC US)
Poa fendleriana W N American
Poa strictiramea Brewster c Endemic Mont
Polypogon elongatus American Trop/Subtr
Polypogon interruptus American (W American)
Pseudoroegneria spicata W N American
Schedonnardus paniculatus Prairie
Schizachyrium cirratum Madrean (+N S America)
Schizachyrium sanguineum Trop/Subtr/Warm
Schizachyrium scoparium N American
Schizachyrium spadiceum Tr-Pecos-Coahuila
Scleropogon brevifolius Madrean-Mesoam
Setaria grisebachii Madrean-Mesoam
Setaria leucopila SWC US-E Madrean
Setaria parviflora Trop/Subtr-Warm Temperate
Setaria reverchonii SC US
Setaria scheelei Chihuahuan-Tamaulipan
Setaria villosissima Chihuahuan very local
Sorghastrum nutans American
Sphenopholis intermedia N American
Sphenopholis obtusata N American
Sporobolus airoides W N American (US)
Sporobolus contractus J Davis & Presicdio cc. SW US
Sporobolus cryptandrus N American
Sporobolus flexuosus SW US
Sporobolus pyramidatus American
Sporobolus texanus SWC US
Sporobolus wrightii Madrean wide
Tragus berteronianus Trop/Subtr
Trichloris crinita Amphitropical
Tridens albescens S Prairie (SC US)
Tridens eragrostoides Gulf Coast-Tamaulipan-N Chihuahuan
Tridens muticus SWC US-Chihuahuan
Tripsacum dactyloides E N American-Mesoam-NW S American
Trisetum interruptum SWC US (S Prairie-Gulf Coast ?)
Urochloa arizonica Sonoran wide-Mexican Highlands
Urochloa fusca American Trop/Subtr
Vulpia octoflora N American

POLEMONIACEAE: 10/4

Gilia stewartii Chihuahuan wide
Giliastrum acerosum SWC US
Giliastrum incisum Chihuahuan wide
Giliastrum insigne Tr-Pecos-Coahuila
Ipomopsis aggregata W N American
Ipomopsis havardii Tr-Pecos-Coahuila
Ipomopsis laxiflora SWC US
Ipomopsis longiflora SWC US-E Prairie
Ipomopsis pumila WC US
Phlox nana Apachian

POLYGALACEAE: 9/1
Polygala alba Prairie-Madrean wide
Polygala barbeyana Madrean wide
Polygala hemipterocarpa J Davis c. Sonoran-Chihuahuan
Polygala lindheimeri Sonoran-Chihuahuan
Polygala macradenia Sonoran wide-Mexican Highlands
Polygala maravillasensis Chihuahuan local
Polygala nudata Chihuahuan
Polygala obscura J Davis c. N Sonoran-Chihuahuan
Polygala scoparioides Sonoran-Chihuahuan wide

POLYGONACEAE: 20/3
Eriogonum abertianum (S Great Basin)-Sonoran-Chihuahuan
Eriogonum alatum WC US
Eriogonum annuum Prairie
Eriogonum havardii N Chihuahuan
Eriogonum hemipterum Tr-Pecos-Coahuila
Eriogonum hieraciifolium S Great Basin-Chihuahuan low Mount
Eriogonum jamesii SWC US
Eriogonum longifolium Pecos c SC US
Eriogonum nealleyi Pecos c. S TX Endemic
Eriogonum polycladon J Davis c. S Great Basin-Sonoran
Eriogonum rotundifolium Chihuahuan
Eriogonum suffruticosum Tans Pecos Endemic
Eriogonum tenellum Colorado, E New Mexico, W OK, N, W, C& SW TX ?
Eriogonum wrightii N Madrean
Polygonum longistylum var. *omissum ?*
Polygonum punctatum American
Polygonum pensylvanicum N American-Mesoam
Polygonum glabrum Atlantic-Gulf Coast-Caribbean (+Madagascar&China)
Polygonum hydropiperoides American
Rumex maritimus N &W N American

POLYPODIACEAE: 1/1
Pleopeltis riograndensis N Sonoran-Chihuahuan

PONTEDERIACEAE: 3/1
Heteranthera dubia N American
Heteranthera reniformis Mesoam-S American
Heteranthera rotundifolia Mesoam-S American

PORTULACACEAE: 9/4
Phemeranthus aurantiacus Apacian-E Madrean
Phemeranthus brevicaulis N Chihuahuan+ NE NM
Phemeranthus longipes ? (Apachian)-Chihuahuan-Tamaulipan
Phemeranthus parviflorus Prairie
Portulaca pilosa Trop/Subtr
Portulaca suffrutescens Sonoran
Portulaca umbraticola American Trop/Subtr
Talinopsis frutescens Chihuahuan
Talinum paniculatum American

POTAMOGETONACEAE: 2/1
Potamogeton foliosus Presidio c. N American
Potamogeton nodosus Polichorous

PRIMULACEAE: 3/2
Androsace occidentalis N American
Androsace septentrionalis Holarctical
Samolus ebracteatus Mesoam-Madrean

PTERIDACEAE: 33/8
Adiantum capillus-veneris Trop/Subtr/Warm
Argyrochosma limitanea Madrean wide
Argyrochosma microphylla Sonoran wide
Astrolepis cochisensis Madrean wide
Astrolepis integerrima Madrean wide
Astrolepis sinuata American Trop/Subtr/Warm
Astrolepis windhamii Sonoran
Bommeria hispida Sonoran
Cheilanthes alabamensis Appalachian-N Madrean
Cheilanthes bonariensis American-African
Cheilanthes eatonii Madrean wide
Cheilanthes feei N American
Cheilanthes horridula E Madrean
Cheilanthes kaulfussii Mesoam-Central American
Cheilanthes lendigera Mesoam-Central American
Cheilanthes lindheimeri Madrean
Cheilanthes tomentosa S& SE N American
Cheilanthes villosa Sonoran-Chihuahuan
Cheilanthes wrightii Sonoran
Notholaena aliena Chihuahuan ?
Notholaena aschenborniana E Madrean
Notholaena copelandii E Madrean
Notholaena grayi Sonoran-Chihuahuan
Notholaena greggii Chihuahuan
Notholaena nealleyi E Madrean ?
Notholaena neglecta Chihuahuan
Notholaena standleyi E Madrean-Apachian
Pellaea atropurpurea N American-Mesoam
Pellaea intermedia Sonoran-Chihuahuan
Pellaea ovata Mesoam-S American
Pellaea ternifolia Mesoam-S American
Pellaea truncata J Davis c. N Madrean
Pellaea wrightiana ? (N American, sporadic)

RAFFLESIACEAE: 1/1
Pilostyles thurberi SW N American disjunct

RANUNCULACEAE: 11/7
Anemone berlandieri SC-SE US
Anemone tuberosa N Madrean
Aquilegia chrysantha Apachian-N Sonoran SW US
Aquilegia longissima N Sonoran ? N Chihuahuan ?
Clematis drummondii Sonoran wide
Clematis pitcheri Illinoan-TX. EN American (wide)
Delphinium wootonii Apachian
Delphinium madrense Chihuahuan-Tamaulipan
Myosurus minimus Holarctical
Ranunculus sceleratus Holarctical
Thalictrum fendleri Presidio, J Davis W N American

RESEDACEAE: 1/1
Oligomeris linifolia Madro (N Madro)-Tethyan ?

RHAMNACEAE: 11/9
Adolphia infesta C-S Madrean (Mexican Highlands-Sonoran)
Ceanothus greggii Madrean Mont
Colubrina texensis Chihuahuan

Condalia ericoides Sonoran Mont
Condalia viridis Chihuahuan (+Sonora)
Condalia warnockii Sonoran
Frangula betulifolia Madrean wide Mont
Karwinskia humboldtiana Caribbean-Sonoran
Rhamnus serrata C-S Madrean Mont
Sageretia wrightii Sonoran Mont
Ziziphus obtusifolia Madrean

ROSACEAE: 12/9
Cercocarpus montanus W N American Mont
Crataegus tracyi S TX-Coahuila
Fallugia paradoxa NC Madrean
Holodiscus dumosus W N American (not coastal)
Malacomeles denticulata ? Mesoam Mont disjunct
Petrophyton caespitosum W N American
Prunus havardii Tr-Pecos Endemic Mont
Prunus murrayana Tr-Pecos Endemic Mont
Prunus serotina ? American-European
Prunus virginiana J Davis c. N American (not SE)
Purshia ericifolia Tr-Pecos-Coahuila
Vauquelinia corymbosa Chihuahuan-Tamaulipan disjunct Mont

RUBIACEAE: 17/6
Bouvardia ternifolia Mesoam Mont
Cephalanthus occidentalis N American (not Central)
Galium correllii Chihuahuan local
Galium mexicanum Mesoam
Galium microphyllum Madrean (not Cal)
Galium proliferum N Madrean
Galium uncinulatum Mesoam
Galium virgatum SC US (Comanchian)
Galium wrightii N Madrean Mont (mostly Sonoran)
Hedyotis intricata Chihuahuan
Houstonia acerosa S Rocky M-Chihuahuan Mont
Houstonia humifusa SC US
Houstonia wrightii J Davis c. NW Sonoran
Stenaria butterwickiae Tr-Pecos Endemic
Stenaria mullerae N Chihuahuan local
Stenaria nigricans E N American
Stenaria rupicola N Chihuahuan (Tr-Pecos ?)

RUTACEAE: 4/4
Choisya dumosa Sonoran
Ptelea trifoliata N American-European
Thamnosma texana N Sonoran (+Chihuahuan)
Zanthoxylum parvum Tr-Pecos Endemic Mont

SALICACEAE: 6/1
Salix amygdaloides Presidio c. N American
Salix exigua W N American
Salix gooddingii N Madrean
Salix lasiolepis W N American
Salix nigra E N American
Salix taxifolia Madrean

SAPINDACEAE: 2/2
Sapindus saponaria Trop/Subtr
Ungnadia speciosa Chihuahuan wide ? (+SCW Africa+SW China)

SAPOTACEAE: 1/1
Sideroxylon lanuginosum SC& SE US

SAURURACEAE: 1/1
Anemopsis californica W Madrean

SAXIFRAGACEAE: 1/1
Heuchera rubescens W Madrean

SCROPHULARIACEAE: 29/13
Agalinis calycina Chihuahuan local
Bacopa monnieri Trop/Subtr
Bacopa rotundifolia ? American temperate
Buchnera americana E N American
Castilleja sessiliflora Prairie
Castilleja mexicana Chihuahuan
Castilleja integra S Rocky M-W Madrean
Castilleja lanata Madrean
Castilleja rigida Chihuahuan
Epixiphium wislizeni SWC US
Leucophyllum candidum Chihuahuan
Leucophyllum frutescens Chihuahuan-Tamaulipan
Leucophyllum minus Chihuahuan
Maurandella antirrhiniflora Mesoam-Madrean
Mecardonia procumbens American Trop/Subtr
Mimulus dentilobus W Madrean
Mimulus glabratus American
Nuttallanthus texanus N American
Penstemon ambiguus SWC US
Penstemon baccharifolius Chihuahuan
Penstemon barbatus SW US-Madrean Mont
Penstemon dasyphyllus Sonoran-Chihuahuan (W)
Penstemon fendleri SWC US
Penstemon havardii Tr-Pecos-Coahuila Mont
Penstemon jamesii Apachian
Penstemon ramosus Madrean
Penstemon wrightii Tr-Pecos Endemic
Seymeria scabra Chihuahuan
Veronica peregrina Polichorous

SELAGINELLACEAE: 9/1
Selaginella arizonica Sonoran
Selaginella lepidophylla E&S Madrean Mont
Selaginella mutica Rocky M
Selaginella peruviana W American
Selaginella pilifera Tr-Pecos-Queretaro disjunct
Selaginella rupincola Mexican Highlands-Sonoran Mont
Selaginella underwoodii W N American (Rocky M)
Selaginella viridissima Tr-Pecos-Coahuila
Selaginella wrightii Chihuahuan-Tamaulipan

SIMAROUBACEAE: 1/1
Holacantha stewartii Chihuahuan

SOLANACEAE: 32/10
Calibrachoa parviflora American (SN, Mesoam)
Chamaesaracha coniodes SC N American
Chamaesaracha coronopus SW US wide-N Mexico
Chamaesaracha pallida Chihuahuan
Chamaesaracha sordida SWC N American
Chamaesaracha villosa Chihuahuan
Datura quercifolia ?

Datura wrightii N American (mostly W)
Lycium berlandieri Sonoran-Chihuahuan wide
Lycium pallidum SW US
Lycium puberulum Chihuahuan
Lycium texanum Tr-Pecos Endemic
Lycium torreyi N Madrean
Margaranthus solanaceus Madrean
Nectouxia formosa CS Madrean
Nicotiana glauca SC American
Nicotiana obtusifolia Madrean (N+W)
Nicotiana repanda Chihuahuan ?
Physalis angulata American Trop/Subtr
Physalis cinerascens SC N American-Mesoam
Physalis hederifolia Madrean-Prairie
Physalis heterophylla N American
Physalis mollis SE N American
Quincula lobata SWC N America
Solanum citrullifolium ?
Solanum davisense Tr-Pecos-Coahuila
Solanum douglasii American Trop/Subtr
Solanum elaeagnifolium American
Solanum leptosepalum Tr-Pecos-Coahuila
Solanum ptychanthum N American
Solanum tenuipes Chihuahuan
Solanum triquetrum Chihuahuan-Tamaulipan

STERCULIACEAE: 4/1
Ayenia filiformis Sonoran
Ayenia microphylla Sonoran-Chihuahuan
Ayenia pilosa Tamaulipan
Melochia pyramidata American Trop/Subtr

THELYPTERIDACEAE: 1/1
Thelypteris ovata Gulf Coast-Caribbean

TYPHACEAE: 1/1
Typha domingensis Trop/Subtr

ULMACEAE: 3/1
Celtis pallida Torr. Mesoam-S American
Celtis laevigata EN American
Celtis reticulata W N American wide (not Pacific)

URTICACEAE: 1/1
Parietaria pensylvanica N American

VERBENACEAE: 21/8
Aloysia gratissima Amphitropical
Aloysia wrightii Sonoran wide
Bouchea linifolia Chihuahuan (S TX- Coahuila)
Bouchea spathulata Chihuahuan (Tr-Pecos-Coahuila)
Glandularia bipinnatifida N American (Prairie)
Glandularia pumila SC US
Glandularia quandrangulata Chihuahuan-Tamaulipan
Lippia graveolens Mesoam-C American
Lantana achyranthifolia Mesoam-S American (subtr)
Lantana urticoides ? Madrean with radiations
Phyla cuneifolia WC US. Prairie
Phyla fruticosa American Trop/Subtr
Phyla nodiflora American Trop/Subtr
Tetraclea coulteri Sonoran wide
Verbena bracteata J Davis & Presidio cc. N American
Verbena canescens E Madrean
Verbena halei E Madrean-Gulf Coast
Verbena neomexicana Sonoran
Verbena perennis Sonoran
Verbena plicata SWC US
Verbena scabra Mesoam

VIOLACEAE: 1/1
Hybanthus verticillatus SWC US-Prairie

VISCACEAE: 6/1
Phoradendron coryae Sonoran
Phoradendron hawksworthii N Chihuahuan
Phoradendron juniperinum W N American
Phoradendron macrophyllum California-Sonoran
Phoradendron tomentosum E-S N American
Phoradendron villosum ?

VITACEAE: 2/2
Cissus trifoliata Mesoam-S N American
Vitis arizonica Madrean wide

ZANNICHELLIACEAE: 1/1
Zannichellia palustris Polichorous

ZYGOPHYLLACEAE: 8/4
Guajacum angustifolium Chihuahuan-Tamaulipan
Kallstroemia californica N & W Madrean
Kallstroemia grandiflora W Madrean
Kallstroemia hirsutissima Sonoran-Chihuahuan
Kallstroemia parviflora Madrean wide-Amphitropical (Peru)
Kallstroemia perennans SW TX Endemic
Larrea tridentata Madrean wide (W)
Peganum mexicanum Chihuahuan-S Sonora

ACKNOWLEDGMENTS

I deeply thank Michael Powell and Steven McLaughlin for review and helpful comments, S. McLaughlin, S. Manchester, and M. Lavin for the offprints of their works, and my husband A. Karabegov for the help with the wording. This work was supported by a grant from Sam Taylor Foundation. I am very thankful to all the contributors to the Tropicos and Flora Texas Consortium as well as other botanical databases for the data available online. My deepest gratitude goes to John Kartesz and Christopher Meacham for the software, *Synthesis of the North American Flora*.

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BOOK NOTICE

Flora of China Editorial Committee. 2008 (April). **Flora of China, Vol. 11. Oxalidaceae through Aceraceae.** (ISBN Vol. 11: 978-1-930723-73-3, hbk.). Science Press (Beijing) and Missouri Botanical Garden Press (St. Louis), P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. (**Orders:** www.mbgpress.org, mbgpress@mobot.org, 1-877-271-1930). $125.00, 622 pp., 8 3/4" × 11 1/4".

From the publishers.—"Thirty-five plant families are described in this volume. Among these, the Aceraceae include 99 species of maple; the Anacardiaceae contain the cashew nut and mango; the Aquifoliaceae comprise 204 species of holly; the Buxaceae include the boxwoods; the Celastraceae include *Euonymus*, several species of which are ornamentals; the Euphorbiaceae, or spurge family, contain some 400 species in 75 genera, including rubber, which is widely cultivated in tropical areas for its latex; the Geraniaceae comprise mainly the cranesbills, including several ornamental species; the Linaceae contain flax, which is cultivated for its stem fiber and seed oil; the Rutaceae include the commercially important citrus fruits as well as Sichuan pepper, *Zanthoxylum*; and the Simaroubaceae include the tree of heaven, which is an invasive alien in some parts of the world."

Editors Wu Zhengyi, Peter H. Raven, and Hong Deyuan state, "[This] is the 15th of a 25-volume work. It includes 35 families, 212 genera, and 1444 species, among which six genera and 615 species (42.6%) are endemic to China, and one family, 17 genera and 49 species (3.4%) are introduced to China." The families covered are (in alphabetical order): Aceraceae, Anacardiaceae, Aquifoliaceae, Biebersteiniaceae, Burseraceae, Buxaceae, Callitrichaceae, Cardiopteridaceae, Celastraceae, Cneoraceae, Coriariaceae, Daphniphyllaceae, Dichapetalaceae, Dipentodontaceae, Erythroxylaceae, Euphorbiaceae, Geraniaceae, Icacinaceae, Linaceae, Malpighiaceae, Meliaceae, Nitrariaceae, Oxalidaceae, Pandaceae, Peganaceae, Plagiopteraceae, Polygalaceae, Rutaceae, Salvadoraceae, Simaroubaceae, Staphyleaceae, Surianaceae, Tapisciaceae, Tropaeolaceae, and Zygophyllaceae. Also included in the text: Preface, Introduction, Acknowledgments, List of Nomenclatural Novelties Published in this Volume of the *Flora of China*, Index to Chinese Names, Index to Pinyin Names, Index to Scientific Names, Index to Families in the *Flora of China* and the *Flora Reipublicae Popularis Sinicae,* and Published Volumes of the *Flora of China* and the *Flora of China Illustrations*. A large map of China and its 35 Administrative Divisions is printed on both the inside front cover/front endpaper and the inside back cover/back endpaper.

J. Bot. Res. Inst. Texas 3(1): 442. 2009

ANNOTATED CHECKLIST OF THE VASCULAR FLORA OF THE MENARD CREEK CORRIDOR UNIT OF THE BIG THICKET NATIONAL PRESERVE, POLK, LIBERTY, AND HARDIN COUNTIES, TEXAS

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ABSTRACT

An annotated, vouchered checklist is provided of the vascular plant taxa of the 1,537 hectare Menard Creek Corridor Unit, Big Thicket National Preserve, in Polk, Liberty, and Hardin counties, Texas. Documented for the unit are 689 taxa of which 70 (10%) are exotics.

RESUMEN

Se realiza un catálogo con anotaciones y testigos de los taxa de plantas vasculares de las 1,537 hectáreas de la Menard Creek Corridor Unit, Big Thicket National Preserve, en los condados de Polk, Liberty, y Hardin, Texas. Se documentan para la unidad 689 taxa de los que 70 (10%) son exóticos.

INTRODUCTION

This is the 7th part of an inventory, based upon available voucher specimens, of the vascular flora of the Big Thicket National Preserve, southeastern Texas. In six previous papers, we provided annotated checklists of the Hickory Creek, Turkey Creek, Big Sandy Creek, Lance Rosier, Beech Creek, and Loblolly units (MacRoberts et al. 2002; Brown et al. 2005, 2006a, 2008, 2008b). In this paper, we provide an annotated checklist of the Menard Creek Corridor Unit.

SITE AND METHODS

The Big Thicket is located in the West Gulf Coastal Plain in southeastern Texas (see Diggs et al. 2006 for literature and description). Peacock (1994) reported 12 units for the Big Thicket Biological Preserve. Since then the Big Sandy Creek Corridor (1,798 hectares), the Canyonlands (350 hectares), and the Village Creek Corridor (2,059) have been added. The addition of these 3 units has added 4,207 hectares to the 34,000 reported by Peacock in 1994. However, Deanna Boensch (per. comm.) indicated the total hectares are now 40,088. The units range from 222 to 10,000 hectares and are scattered over 7 Texas counties. The Menard Creek Corridor Unit (1,537 hectares) follows Menard Creek through parts of Polk, Liberty, and Hardin counties (Fig. 1). It is located on the Deweyville/Fluviatile formation within a small channel and narrow bottomlands consisting of Bibb sandy loam and Hatliff fine sandy loam soils that are frequently flooded (Deshotels 1978; Aronow 1981; Shelby et al. 1992; Griffith 1996). Elevation ranges from about 46 meters at the Highway 943 bridge over Menard Creek in Polk County to 13 meters at the confluence with the Trinity River in Liberty County. The unit consists of bottomland forest next to the stream and lower slope-hardwood pine forest and upper slope pine-oak forest (Harcombe & Marks 1979; Marks & Harcombe 1981). Some other small distinct habitats that are mostly in Liberty County are Beech-Magnolia slopes where *Prenanthes*

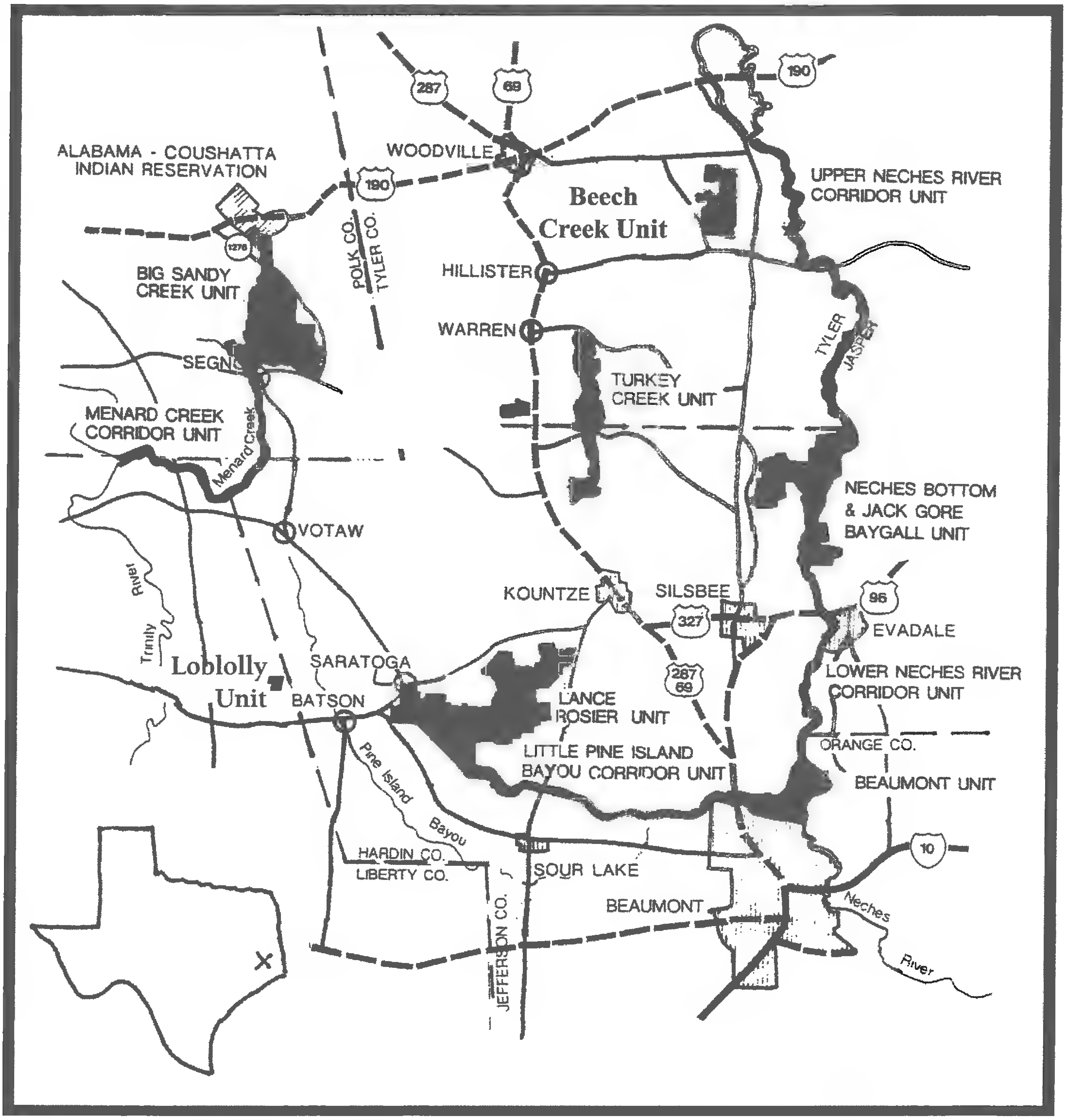

Fig. 1. Location of the Menard Creek Corridor Unit, Big Thicket National Preserve, Texas.

barbata, Viburnum acerifolium, Cynoglossum virginianum, and *Carex abscondita* are found; areas of deep sands where *Sida lindheimeri, Setaria corrugata, Mitracarpus hirta*, and *Silene subciliata* grow; alkaline soils with heliophyte plants such as *Verbesina helianthoides, Stenanthium gramineum, Liatris asper, Phyllanthus pudens*, and the 2 *Silphium* taxa. Another small habitat with a distinct flora is the alluvial soil exposed by receding water during late summer and fall at the confluence of Menard Creek and the Trinity River. Some of the plants only or mostly on these drawn-down sites are *Fimbristylis vahlii, Eragrostis reptans, Leptochloa panicea* subsp. *mucronata, Cyperus squarrosus, Cyperus odoratus, Eragrostis japonica, Marsilea vestita, Panicum virgatum*, and *Spermacoce glabra*.

Like all units of the Big Thicket National Preserve, the Menard Creek Corridor Unit had not previously been the subject of a detailed floristic inventory.

Because our purpose is to produce a list of taxa known to occur on the Menard Creek Corridor Unit, a vouchered specimen was considered to be the only evidence acceptable for inclusion in the list. In all, 1,137 herbarium specimens form the data for this report. All specimens have been annotated by Larry Brown.

Larry Brown collected 1,020 specimens beginning in the late 1980s and early 1990s and during 16 field days in 2007 and 2008. Geraldine Watson collected 106 specimens over several years in the late 1970s and early 1980s. The collection total of a few others is 13 and is designated by the appropriate abbreviation below.

In most cases, nomenclature follows Jones et al. (1997), Kartesz (1999), and Diggs et al. (2006). In cases of multiple collections, no more than 4 are listed for each taxon.

RESULTS

The following is an annotated list of the Menard Creek Corridor Unit taxa. Abbreviations used are given below.

CP = Charles Peterson. His one Azalea collection is at SBSC.
DB = Deanna Boensch. Big Thicket fire ecologist. She collected with LB and those are at TAES.
GW = Geraldine Watson. Her specimens are at TAES.
JL = Joe Liggio. His orchid specimens are at SBSC.
JS = Jeff Schultz. His one orchid collection is at SBSC.
LB = Larry Brown. His specimens with collection numbers above 23,000 are at TAES and those with numbers below 23,000 are at SBSC.
MM = Barbara and Michael MacRoberts. Their specimens are at TAES.
PR = Paul Roling. His collections are at TAES.
SH = Shawn Harper (Grandson of LB).
SM = Sam Harper (Grandson of LB).
WH = Walter Hesson. His one fern collection is at SBSC.
WRC = Bill Carr. His specimens are at TEX.
***** = exotic
+ = see note at end of list.
! = taxa with this symbol have only been collected in the Menard Creek Unit when compared with the 7other surveyed units which includes a preliminary species list of the Jack Gore-Neches Bottom unit.
A collection number followed by a (P) is from Polk County. A collection number followed by (H) was collected in Hardin County. All others are from Liberty County.

Acanthaceae
!*Dicliptera brachiata* (Pursh) Spreng., GW 3293, LB 32845
Hygrophila lacustris (Schlecht. & Cham.) Nees, LB 18779, 26104 (P)
Justicia ovata (Walter) Landau var. *lanceolata* (Chapm.) Long, LB 32694
Ruellia caroliniensis (Walter) Steud., LB 32913 (P)
!*Ruellia pedunculata* Torr. ex A. Gray, PR s.n.
!*Ruellia strepens* L., LB 18705, 33097

Aceraceae
!*Acer negundo* L., GW 3236; LB 32523
Acer rubrum L., LB 33147, 26111 (P)

Agavaceae
Manfreda virginica (L.) Rose, LB 32563, 32879

Alismataceae
Sagittaria latifolia Willd. LBJL 32970, 32982 (P), LB 26113 (P), 5829 (P)
!*Sagittaria montevidensis* Cham. & Schltdl. subsp. *calycina* (Engelm.) Bogin, LB 18831

Alliaceae
Allium canadense L. var. *canadense*, LBSH 33219
Allium canadense L. var. *mobilense* (Regel) Ownbey, LBSH, 33434 (P)
Nothoscordum bivalve (L.) Britton, LB 32847

Amaranthaceae
!*Amaranthus tuberculatus* (Moq.) Sauer (including *A. rudis* Sauer), LB 18827; LBJL 32985
Froelichia floridana (Nutt.) Moq., LB 28810 (SBSC)
!*Iresine rhizomatosa* Standl., LB 32884

Anacardiaceae
Rhus copallinum L., LB 32700
Toxicodendron radicans (L.) Kuntze, LB 32528

Annonaceae
Asimina parviflora (Michx.) Dunal, LB 32574; LBSH (H)

Apiaceae
Chaerophyllum tainturieri Hook. var. *tainturieri*, LBSH 33212
Cicuta maculata L., LBSM 33547
**Cyclospermum leptophyllum* (Pers.) Sprague ex Britton & P. Wilson, LBSM 33542
Cynosciadium digitatum DC., GW 3247, 3255; LBSH 33419
!*Daucus pusillus* Michx., GW 3260
!*Eryngium hookeri* Walp., LB 32919
Eryngium prostratum Nutt. ex DC., LB 18616
Hydrocotyle verticillata Thunb., LB 28243 (P)
Limnosciadium pumilum (DC.) Mathias & Constance, LBSH 33420
Ptilimnium capillaceum (Michx.) Raf., LBSH 33415
Sanicula canadensis L., LB 32505; LBSH 33405
Spermolepis divaricata (Walter) Raf., LBPR 33356
!*Spermolepis inermis* (Nutt.) Mathias & Constance, LBSH 33451(P)
Thaspium trifoliatum (L.) A. Gray var. *aureum* Britton, GW 247; LB 18477, 32691; LBSH 33388
!**Torilis arvensis* (Huds.) Link, GW 3248; LBDB 33655
Trepocarpus aethusae Nutt. ex DC., GW 3262; LBSH 33245

Apocynaceae
Amsonia tabernaemontana Walter, GW 3344
Trachelospermum difforme (Walter) A. Gray, LB 32714 (P), 32823, 25185

Aquifoliaceae
Ilex ambigua (Michx.) Torr., LB 18846; LBJL 32974
Ilex decidua Walter, LB 25179, 32908 (P); GW 3296a
Ilex longipes Chapm. ex Trel., GW 3157; LBJL 32983 (P), LB 33128; LBSH 33461 (P)
Ilex opaca Aiton, LB 32534, 22564
Ilex vomitoria Aiton, LB 32636

Araceae
Arisaema dracontium (L.) Schott., LB 23880; LBPR 33361
Arisaema triphyllum (L.) Schott., LB 18525, 23880a, 27734 (P); LBJL 32964

Araliaceae
Aralia spinosa L., LBSH 33332
Hedera helix L., LBSH 33399

Arecaceae
Sabal minor (Jacq.) Pers., LB 32856

Aristolochiaceae
Aristolochia serpentaria L., LB 33168 (P)

Asclepiadaceae
Asclepias perennis Walter, LB 18574
Asclepias tuberosa L., LB 32565
Asclepias variegata L., LBPR 33351
Matelea gonocarpos (Walter) Shinners, LB 32519

Aspleniaceae
Asplenium platyneuron (L.) Britton, Sterns & Poggenb., GW 3217; LB 32717

Asteraceae
Acmella repens (Walter) Richard, LB 18860
Ageratina altissima (L.) R. King & H. Rob. var. *altissima*, LB18832, 33149, 33174 (P); LBJL 32957
Ambrosia artemisiifolia L., LB 32854
Ambrosia trifida L., LB 32844, 32820, 32874
Arnoglossum ovatum (Walter) H. Rob. LB 15403
!*Arnoglossum plantagineum* Raf., LBSH 33323
Baccharis halimifolia L., GW 3297; LB 32859
Bidens aristosa (Michx.) Britton, LB 18553, 32920, 33105; LBJL 32954
Bidens bipinnata L., GW 3286; LB 32930, 32916
Bidens discoidea (Torr. & A. Gray) Britton, LB 18820b (P)
Bidens frondosa L., LB 18511, 18859,18241
Bradburia pilosa (Nutt.) Semple, LB 32552,18743, 26108 (P)
!*Calyptocarpus vialis* Less., LBSH 33372
Chrysopsis mariana (L.) Elliott, LBJL 32978; LBSM 33540
Cirsium horridulum Michx. var. *megacanthum* (Nutt.) D.J. Keil, LBSH 33386
Conoclinium coelestinum (L.) DC., LB 32878
Conyza bonariensis (L.) Cronquist, GW 3251
Conyza canadensis (L.) Cronquist, LB 32654
!*Coreopsis basalis* (A. Dietr.) S.F. Blake, GW 3277; LB 18606, 32463
Coreopsis lanceolata L., LBSH 33411
Coreopsis tinctoria Nutt. var. *tinctoria*, LB 32938; LBSM 33525 (P)
Croptilon divaricatum (Nutt.) Raf., LB 32575, 32576
Echinacea sanguinea Nutt., LBSH 33516
Eclipta prostrata (L.) L., LB 18856, 32825
Elephantopus carolinianus Raeusch, LB 33155 (P)
Elephantopus nudatus A. Gray, GW 3284
Elephantopus tomentosus L., LB 32575, 18726
Erechtites hieraciifolia (L.) Raf. ex DC., LB 32747
Erigeron annuus (L.) Pers., GW 3276; LBSH 33377, 33443 (P); LBSM 33544
Erigeron philadelphicus L., LBSH 33467
Erigeron strigosus Muhl. ex Willd., GW 3267; LBSH 33512, 33468
Erigeron tenuis Torr. & A. Gray, LBPR 33353; LBSH 33392, 33416
Eupatorium capillifolium (Lam.) Small, LB 33129
+*Eupatorium semiserratum* DC., LB 32675, 33153
Eupatorium serotinum Michx., LB 32877
Eurybia hemispherica (Alexander) G.L. Nesom, GW 3473; LB 32812
Euthamia leptocephala (Torr. & A. Gray.) Greene, LB 32753, 32821
Gaillardia pulchella Foug. var. *pulchella*, LB 32688
Gamochaeta coarctata (Willd.) Kerguelen, LBSH 33378
Gamochaeta pensylvanica (Willd.) Cabrera, LBSH 33244 (P)
Gamochaeta purpurea (L.) Cabrera, LBSH 33431,33449a (P)
Helenium amarum (Raf.) H. Rock var. *amarum*, LB 33260, 32706, 32928; LBSH 33438 (P)
Helianthus hirsutus Raf., GW 3512; LB 32705
Heterotheca subaxillaris (Lam.) Britton & Rusby, LB 32924
Hieracium gronovii L., GW 3311; LB 32504
Iva annua L., LB 32906 (P)
Krigia cespitosa (Raf.) K.L. Chambers var. *cespitosa*, GW 3369; LBSH 33240
Krigia cespitosa (Raf.) K.L. Chambers var. *Gracilis* (DC.) K.L. Chambers, LBSH 33247 (P)
!*Krigia dandelion* (L.) Nutt., LBSH 33325
Krigia virginica (L.) Willd. LBSH 33316
Krigia wrightii (A. Gray) K.L. Chambers ex K.J. Kim LBSH 33313
Lactuca canadensis L., LB 32656
Lactuca floridana (L.) Gaertn., LB 32846
!*Lactuca hirsuta* Muhl., LBSM 33535
!*Liatris asper* Michx., GW 3503, 3504, 3505; LB 32562
Mikania scandens (L.) Willd., LB 32750
Packera glabella (Poir.) C. Jeffrey, LBSH 33225a, 33231
Packera obovata (Muhl. ex Willd.) W.A. Weber & Á. Löve, GW 3324; LBSH 33321
Packera tampicana (DC.) C. Jeffrey, LB 18532
Pluchea camphorata (L.) DC., LBJL 32977
Pluchea foetida (L.) DC., LB 32939
!+*Prenanthes barbata* (Torr. & A. Gray) W.L. Milstead ex Cronquist, LBJL 32972
Pyrrhopappus carolinianus (Walter) DC., LB 33103
Pyrrhopappus pauciflorus (D. Don) DC., LBSH 33249 (P)
Rudbeckia hirta L., LB 32697
!*Silphium asteriscus* L. var. *asteriscus* L., LB 32744
!*Silphium asteriscus* L. var. *simpsonii* (Greene) J.S. Clevinger, LBSM 33538
Solidago altissima L., LB 32850
Solidago ludoviciana (A. Gray) Small, LB 5839a

Solidago rugosa Mill. var. *asper* (Aiton) Fernald, LB 18854, 18865
Solidago tortifolia Elliott, LBJL 32979
**Soliva sessilis* Ruiz & Pavon, LBPR 33338
**Sonchus asper* (L.) Hill, LBSH 33242
**Sonchus oleraceus* L., LBSH 32264
Smallanthus uvedalia K. Mack. ex Small, LB 18707
!*Symphyotrichum drummondii* (Lindl.) G.L. Nesom, LB 32508; GW 3238
Symphyotrichum dumosum (L.) G.L. Nesom, LB 32873, 32872
!*Symphyotrichum ericoides* (L.) G.L. Nesom, LB 33154 (P)
!*Symphyotrichum lanceolatum* (Willd.) G.L. Nesom., LB 33083, 33130, 33133, 33145
Symphyotrichum lateriflorum (L.) Á. Löve & D. Löve, LB 18863, 18862
Symphyotrichum patens (Aiton) G.L. Nesom, LBSM 33541
Symphyotrichum racemosum (Elliott) G.L. Nesom, LB 18826, 19767, 33104; LBJL 32955
+*Verbesina helianthoides* Michx., LB 32568
Verbesina virginica L., LB 32564
Vernonia missurica Raf., LB 26102 (P), 32640; GW 3280
Vernonia texana (A. Gray) Small, LB 32566
Xanthium strumarium L., LB 32826
**Youngia japonica* (L.) DC., GW 3279

Berberidaceae
!**Nandina domestica* Thunb., LB 32830
Podophyllum peltatum L., PR s.n.

Betulaceae
Betula nigra L., LB 18603, 33122 (P), 33159 (P), 28249 (P)
Carpinus caroliniana Walter, LB 18600a
Ostrya virginiana K. Koch, LB 32628

Bignoniaceae
Bignonia capreolata L., LB 32517, 18502, 27743 (P)
Campsis radicans (L.) Seem. ex Bureau, LB 32689
Catalpa bignonioides Walter, LBSH 33460 (P)

Blechnaceae
Woodwardia areolata (L.) T. Moore, LB 26118 (P), 32555, 18520, 18744
Woodwardia virginica (L.) Sm., LB 19025, 33158 (P)

Boraginaceae
Cynoglossum virginianum L., GW 3195, 3239; LBPR 33358
**Heliotropium indicum* L., LB 18825, 32842, 17515 (P)
Heliotropium procumbens Mill., LB 18842, 32887
Myosotis macrosperma Engelm., LB 18497

Brassicaceae
**Cardamine hirsuta* L., LBSH 33205
Cardamine parviflora L. var. *arenicola* (Britton) O.E. Schulz, GW 3204a, 3205
Lepidium virginicum L., LB 32647; LBSH 33317
Rorippa sessiliflora (Nutt.) Hitchc., GW 3189, 3204b; LB 18829, 32899

Buddlejaceae
Polypremum procumbens L., LB 32935

Burmanniaceae
Burmannia biflora L., LB 18778

Callitrichaceae
Callitriche heterophylla Pursh, LBSH 33253 (P)

Campanulaceae
Lobelia appendiculata A. DC., LBPR 33352, 33440 (P); LBSM 33539
Lobelia cardinalis L. var. *cardinalis*, LB 32935
Lobelia puberula Michx., LB 32927; LBJL 32958
Triodanis biflora (Ruiz & Pav.) Greene, LBSH 33457a
!*Triodanis lamprosperma* McVaugh, LBSH 33423, 33456 (P)
Triodanis perfoliata (L.) Nieuwl., GW 3234, 3235; LBSH 33398
**Wahlenbergia marginata* (Thunb.) A. DC., LBSH 33448 (P)

Caprifoliaceae
**Lonicera japonica* Thunb., LB 32718
Lonicera sempervirens L., LBSH 33236
Sambucus nigra L. subsp. *canadensis* (L.) Bollii, LB 32516; LBJL 32962
!*Symphoricarpos orbiculatus* Moench., LB 18529, 18708
Viburnum acerifolium L., 18516, 24130, 33125
Viburnum dentatum L., LB 32634, 32624
Viburnum nudum L., LB 18499
Viburnum rufidulum Raf., LB 32812

Caryophyllaceae
**Cerastium glomeratum* Thuill., LBSH 33208
Loeflingia squarrosa Nutt., LBPR 33355
Sagina decumbens (Elliott) Torr. & A. Gray, LBPR 33353
**Stellaria media* (L.) Vill., LBSH 33222
!*Silene antirrhina* L., LBSH 33447 (P)
!**Silene gallica* L., LBSH 33457 (P)
+*Silene subciliata* Robins., LB 18727, 18162, 32633; LBJL 32953

Celastraceae
Euonymus americana L., LB 32551

Chenopodiaceae
Dysphanis ambrosioides (L.) Mosyakin & Clemants, LB 33138

Cistaceae
Helianthemum georgianum Chapm., LBSH 33511

Commelinaceae
Commelina diffusa Burm. f., LB 32897
Commelina erecta L. var. *angustifolia* (Michx.) Fernald, LB 32653; LBSM 33548
Commelina virginica L., LB 18597, 32893

Convolvulaceae
Dichondra carolinensis Michx., LB 32837
Evolvulus sericeus Sw., GW 3271
Ipomoea cordatotriloba Dennst. var. *cordatotriloba*, LB 32849
Ipomoea lacunosa L., LB 32827

Cornaceae
!*Cornus drummondii* C.A. Mey., GW 3254; LB 32524, 18530
Cornus florida L., LB 32543, 18595
Nyssa aquatica L., LB 18601
Nyssa sylvatica Marshall, LB 32540, 18518, 18735

Crassulaceae
Penthorum sedoides L., LB 18851, 18780

Cucurbitaceae
Cayaponia quinquefolia (Raf.) Shinners, LB 32836
Melothria pendula L., LB 32757

Cupressaceae
Juniperus virginiana L., LBJL 32960
Taxodium distichum (L.) Rich., LB 32631a

Cuscutaceae
Cuscuta gronovii Willd. ex Schult., GW 3294, LB 32929

Cyperaceae
Bulbostylis barbata (Rottb.) C.B. Clarke, LB 28808
Carex abscondita Mack., LB 27762, 29426; LBSM 33537
Carex albicans Willd. ex Spreng. var *australis* (L.H. Bailey) Rettig, LBSH 33374
Carex albolutescens Schwein., LB 18507, 18575
Carex atlantica L.H. Bailey subsp. *capillacea* (L.H. Bailey) Reznicek, LB 27724 (P), 19023; LBSH 33334, 33404 (H)
Carex basiantha Steud., LB 27765, 29429
Carex blanda Dewey., LB 27759, 27752, 25183
Carex brevior (Dewey) Mack. ex Lunell, LB 18505b
Carex caroliniana Schwein., LB 27740(P); LBSH 33376
Carex cephalophora Muhl. ex Willd., LBPR 33359
Carex cherokeensis Schwein., LB 32506
Carex complanata Torr. & Hook., LB 18523; LBPR 33344
Carex corrugata Fernald, LB 27767, 18534
Carex crebriflora Wiegand, LB 27764, 2774; LBSH 33259 (P), 33369
Carex crus-corvi Shuttlew. ex Kunze, LBSM 33517
Carex debilis Michx. var. *debilis*, LB 27758, 23878, 18491
Carex digitalis Schkuhr ex Willd. var. *floridana* (L.H. Bailey) Naczi & Bryson, LB 27761, 27760, 27756, 27737
Carex festucacea Schkuhr ex Willd., LBPR, 33363; LBSH 33425
Carex flaccosperma Dewey, LB 27749, 27738; LBPR 33362
Carex frankii Kunth, LB 15433(P), 28249 (P)
Carex glaucescens Elliott, LB 33161 (P)
!*Carex hyalina* Boott, LBSM 33523
Carex intumescens Rudge, LB 27722, 18576
Carex joorii L.H. Bailey, LB 18734, 15501, 15441 (P)
Carex leavenworthii Dewey, LB 27766
Carex leptalea Wahlenb. subsp. *harperi* (Fernald) W. Stone, LB 27728(P), 33163 (P); LBJL 19024
Carex longii Mack., LBSH 33389
Carex lupulina Muhl. ex Willd., LBSH 33463 (P)
Carex oxylepis Torr. & Hook., LB 27754, 18537; LBSH 33426
Carex planispicata Naczi, LB 27757; LBPR 33357
Carex reniformis (L.H. Bailey) Small, LBPR 33343; LBSH 33407, 33370, 33429
Carex retroflexa Muhl. ex Willd., LB 18531
Carex striatula Michx., LB 29427, 27755, 18605, 18501
Carex triangularis Boeck., LBPR 33341; LBSH 33381
Carex tribuloides Wahlenb. var. *sangamonensis* Clokey, LB28245 (P), 18507, 24134
!+ *Carex typhina* Michx., LBSM 33518
Cyperus acuminatus Torr. & Hooker ex Torr., LB 32875, 33114 (P)
Cyperus croceus Vahl, LB 28806
Cyperus erythrorhizos Muhl., LB 18839a, 32989
**Cyperus esculentus* L., LB 33109
Cyperus haspan L., LB 18613, 5828 (P), 32677, 18100a (P)
Cyperus odoratus L., LB 18839b, 33085, 33095
Cyperus retroflexus Buckley var. *retroflexus*, LB 32573
Cyperus squarrosus L., LB 33091
!*Cyperus strigosus* L., LB 15500
Cyperus surinamensis Rottb., LB 33146
Cyperus thyrsiflorus Jungh., LB 32824; LBSM 33532
Cyperus virens Michx., LB 32876
Eleocharis microcarpa Torr., LB 32679
Eleocharis montana (Kunth) Roem. & Schult., LB 32285
Eleocharis montevidensis Kunth, LBSH 33414
Eleocharis tuberculosa (Michx.) Romer & Schult., LB 18611, 32676, 15434a (P), 26615 (P)
Fimbristylis autumnalis (L.) Romer & Schult., LB 32902
**Fimbristylis miliacea* (L.) Vahl, LB 32681, 33094
Fimbristylis vahlii (Lam.) Link, LB 18833, 33087,17510 (P), 33111 (P)
Fuirena breviseta Coville, LB 26125 (P)
!*Fuirena pumila* (Torr.) Spreng., LB 22566 (P)
Isolepis carinata Torr., LB 18510
Rhynchospora caduca Elliott, LBSM 33531
Rhynchospora corniculata (Lam.) A. Gray, LBSM 33530
Rhynchospora globularis (Chapm.) Small var. *globularis*, LB 32707
Rhynchospora glomerata (L.) Vahl, LB 15429 (P), 26122 (P), 18741, 32940
Rhynchospora inexpansa (Michx.) Vahl, LB 32936, 15432 (P); WRC 11352
Rhynchospora mixta Britton, LB 28248 (P), 22862 (P); LBJL 32966, 19176
Scirpus cyperinus (L.) Kunth, LBJL 32969
Scleria oligantha Michx., LB 18480
Scleria triglomerata Michx., WRC 11349; LB 20592

Cyrillaceae
Cyrilla racemiflora L., LB 26114 (P), 18873, 33142

Dennstaedtiaceae
Pteridium aquilinum (L.) Kuhn var. *Pseudocaudatum* (Clute) A. Heller, LB 32556

Dioscoreaceae
Dioscorea villosa L., GW 2288, 3194, 3282; LB 32831; LBSH 33230a

Droseraceae
Drosera brevifolia Pursh, LBSH 32262, 33257 (P)

Dryopteridaceae
Athyrium filix-femina (L.) Roth subsp. *asplenioides* (Michx.) Hulten, LB 28250 (P), 32554, 18517, WH s.n.
Onoclea sensibilis L., LB 28246 (P), 27735 (P), 18495, 33108 (P)
Polystichum acrostichoides (Michx.) Schott, LB 29422, 32553, 18515, 18604

Ebenaceae
Diospyros virginiana L., LB 32860

Ericaceae
Rhododendron canescens (Michx.) Sweet, LB 27747 (P), 18748,18487, 32625
Rhododendron viscosum (L.) Torr., LB18512, 20170 (P), 33151(P); CP s.n. (P)

Vaccinium arboreum Marshall, LB 18580, 33173 (P); LBSH 33455 (P)
Vaccinium corymbosum L., LB 32548, 18489, 18586

Euphorbiaceae
Acalypha gracilens A. Gray, GW 3230, 3288
Acalypha rhomboidea Raf., LB 32904 (P), 32946, 33110 (P)
Chamaesyce humistrata (Engelm.) Small, LB 18818a (P)
Chamaesyce maculata (L.) Small, LBDB 33660
Chamaesyce nutans (Lag.) Small, LB 32632a, 32948
Croton capitatus Michx., WRC 11350; LB 32861
Croton glandulosus L. var. *glandulosus*, GW 3291, LB 32941a
Croton monanthogynus Michx., LB 32640
Euphorbia corollata L., LB 32561
Euphorbia dentata Michx., GW 3432; LB 32693
Euphorbia spathulata Lam., LB 18532b
Phyllanthus caroliniensis Walter, LB 18857a, 33115 (P)
!*Phyllanthus pudens* Wheeler, LB 18818b (P)
Phyllanthus urinaria L., WRC 11355; LB 18866
Sebastiania fruticosa (Bartr.) Fernald, LB 27732 (P), 32547, 18485, 18598
Triadica sebiferum (L.) Small, LB 32544

Fabaceae
Aeschynomene indica L., LB 17513 (P)
Albizia julibrissin Durazz., LB 32699; LBSM 33543
Baptisia nuttalliana Small, LB 18539, 24237
Centrosema virginianum (L.) Benth., LB 18687
Cercis canadensis L. var. *canadensis*, LB 32754
Chamaecrista fasciculata (Michx.) Greene, LB 18729, 33136
Chamaecrista nictitans Moench, LB 32663
Clitoria mariana L., LB 32743
Crotalaria sagittalis L., LB 18615; LBSH 33452 (P)
Dalea phleoides (Torr. & A. Gray) Shinners var. *phleoides*, GW 3509
!*Desmodium canescens* (L.) DC., LBDB 33653
Desmodium ciliare (Willd.) DC., GW 3313b; LB 32881
Desmodium glabellum (Michx.) DC., GW 3290, 3313a; LB32755, 32817
Desmodium paniculatum (L.) DC., LB 18161, 32922; LBDB 33665
!*Desmodium pauciflorum* (Nutt.) DC., LB 29428
Erythrina herbacea L., LB 32882
Galactia volubilis (L.) Britton, GW 3285, 3304, 3312; LB 18244
Gleditsia triacanthos L., LB 32541
Glottidium vesicarium (Jacq.) Harper, LB 32840
Indigofera suffruticosa Mill., LB 32570, 28805 (SBSC)
Kummerowia striata (Thunb.) Schlindler, LB 32698, 32811a
Lespedeza procumbens Michx., LB 32855, 32880
Lespedeza repens (L.) Barton, LB 32819
Lespedeza virginica (L.) Britton, GW 3511; LBSM 33524; LBDB 33658
!*Medicago arabica* (L.) Huds., LBSH 33223
Medicago lupulina L., GW 3190a, 3219a, LBSH 33210
Medicago polymorpha L., GW 3219b; LBSH 33233a
Mimosa hystricina (Small) B.L. Turner, LB 32858a
Mimosa latidens (Small) B.L. Turner, LBSH 33514
Mimosa strigillosa Torr. & A. Gray, LB 32712 (P), 33090
!*Rhynchosia minima* (L.) DC., LB 32822
Senna marilandica (L.) Link, GW 3227; LB 18828, 32745
Senna obtusifolia (L.) H.S. Irwin & Barneby, LB 18828, 17514 (P)
Sesbania drummondii (Rydb.) Cory, LB 33106
Sesbania herbacea (Mill.) McVaugh, LB 32918
!*Sesbania punicea* Benth., LB 22567 (P)
Sophora affinis Torr. & A. Gray, LB 32503, 33102
Strophostyles helvula (L.) Elliott, LB 32637
Strophostyles umbellata (Willd.) Britton, LB 32719
Stylosanthes biflora (L.) Britton, Sterns, & Poggenb., GW 3305; LB 32811
Trifolium campestre Schreb., LBSH 33227
Trifolium dubium Sibth., LBSH 33251 (P)
Trifolium lappaceum L., LB 29420
Trifolium repens L., GW 3240
!*Trifolium resupinatum* L., GW 3219c
Vicia ludoviciana Nutt. subsp. *leavenworthii* (Torr. & A. Gray) Lassetter & C.R. Gunn., LBSH 33224, 33235a; LB 18443
Vicia ludoviciana Nutt. subsp. *ludoviciana*, LBSH 33230
Vicia minutiflora Dietr., GW 3203, 3225, 3300; LBSH 33217
Vicia sativa L. subsp. *nigra* (L.) Ehrhart, GW 3226; LBSH 33228a
Vicia villosa Roth, LBSH 33246 (P)
Wisteria frutescens (L.) Poir., LB 18478, 18733, 32907 (P)

Fagaceae
Castanea pumila (L.) Mill., LBSH 33512
Fagus grandifolia Ehrh., LBJL 19170; LB 18163, 32557, 27730 (P)
Quercus alba L., LB 32538a, 18483
Quercus falcata Michx., LB 32814
Quercus hemisphaerica Bartram ex Willd., LB 32538, 32987, 28809, 24128
Quercus lyrata Walter, LB 32710 (P), 33124 (P)
Quercus michauxii Nutt., LB 18541; LBJL 32968
Quercus nigra L., LB 32695
Quercus pagoda Raf., LBDB 33657
Quercus phellos L., LB 32815, 27718 (P); LBSH 33462 (P)
Quercus shumardii Buckley, LB 32520; GW 3265
Quercus stellata Wangenh., LB 32756
!*Quercus texana* Buckley, LBPR 33347

Geraniaceae
Geranium carolinianum L., LBSH 33396

Grossulariaceae
Itea virginica L., LB 18488, 33140, 26123 (P); LBJL 32974

Haloragaceae
Proserpinaca palustris L., LB 32275

Hamamelidaceae
Hamamelis virginiana L., LB 32650, 18242, 18608, LBSH 33256 (P)
Liquidambar styraciflua L., LB 29291, 32650

Hippocastanaceae
Aesculus pavia L. var. *pavia*, LBSH 33248 (P)

Hydrophyllaceae
Hydrolea uniflora Raf., LB 18821
!*Nemophila aphylla* (L.) Brummitt, GW 1346, 3190b; LBSH 33215

!*Phacelia hirsuta* Nutt., LB 18442; LBPR 33339

Hypericaceae
Hypericum drummondii (Grev. & Hook.) Torr. & A. Gray, LB 32664
Hypericum galioides Lam., LB 18740
Hypericum hypericoides (L.) Crantz, LB 32629
Hypericum mutilum L., LB 18522, 33151
Triadenum walteri (J.G. Gmel.) Gleason, LB 18684, 27725 (P)
Triadenum tubulosum (Walter) Gleason, LB 32621

Hypoxidaceae
Hypoxis curtisii Rose, LB 18578; LBSH 33391, 33458 (P)

Iridaceae
Herbertia lahue (Molina) Goldblatt, LBSH 33408
!**Iris pseudacorus* L., LB 27739 (P)
Sisyrinchium angustifolium Mill., LB 18505; LBSH 33465
Sisyrinchium rosulatum E.P. Bicknell, GW 3249, LB 18524; LBSH 33387

Juglandaceae
Carya aquatica (Michx. f.) Nutt., LB 18855, 32708 (P)
Carya cordiformis (Wang.) K. Koch, LB 32892
Carya illinoensis (Wang.) K. Koch, LB 32509; LBDB 33654
!*Carya ovata* (Mill.) K. Koch, GW 3191, 3196; LB 32858
Carya texana Buckley, LB 32883
Carya tomentosa (Poir.) Nutt., LB 18481, 33127

Juncaceae
Juncus acuminatus Michx., LBSH 33428
Juncus anthelatus (Wiegand) R.E. Brooks, LBPR
Juncus coriaceus Mack., LB 27748 (P)
Juncus dichotomus Elliott, LBSM 33521
Juncus diffusissimus Buckley, LB 18609; LBSH 33436 (P)
Juncus effusus L., LB 32822
Juncus marginatus Rostk. LBSH 33413, 33427
Juncus scirpoides Lam., LB 18614
Juncus tenuis Willd., LB 27746 (P), 33172 (P)
Juncus validus Coville, LB 18610, 32937

Lamiaceae
Hedeoma hispida Pursh, LBSH 33430; PR s.n.
Hyptis alata (Raf.) Shinners, LB 26119 (P)
!**Lamium amplexicaule* L., LBSH 33221
Lycopus rubellus Moench, GW 3309
Lycopus virginicus L., LB 18850, 32933
Monarda fistulosa L., GW 3510
Monarda punctata L. var. *lasiodonta* A. Gray, LB 18685, 28804, 32932
**Perilla frutescens* (L.) Britton, LB 32619
Prunella vulgaris L., LBPR 33350
Pycnanthemum albescens Torr. & A. Gray, LB 32671
Salvia lyrata L., LBSH 33213
Scutellaria elliptica Muhl., GW 3258a; LB 18593, 18240
Scutellaria integrifolia L., LB 18592; LBSH 33412
!*Scutellaria ovata* Hill, GW 3258b
Scutellaria parvula Michx. var. *parvula*, LBPR 33360; LBSM 33534
Stachys tenuifolia Willd., LB 32620, 26103 (P)
Teucrium canadense L., LB 28251 (P), 33165 (P)
Trichostema dichotomum L., LB 32933

Lauraceae
Persea borbonia (L.) Spreng., LB 29423, 32558
Sassafras albidum (Nutt.) Nees, LB 32549, 18864

Lemnaceae
**Landolta punctata* (G. Mey.) Les & D.J. Crawford, LB 32863

Lentibulariaceae
Utricularia gibba L., LB 26117 (P), 25516 (P)

Linaceae
Linum medium (Planch.) Britton var. *texanum* (Planch.) Fernald, LBSH 33450 (P); PR s.n.
Linum striatum Walter, LB 18612, 24132

Loganiaceae
Gelsemium sempervirens St.-Hil., LB 32638
!*Spigelia texana* (Torr. & A. Gray) A. DC., GW 3259; LB 32838, 18704

Lygodiaceae
**Lygodium japonicum* (Thunb.) Sw., LB 32537; LBSH 33241

Lythraceae
Ammannia coccinea Rottb., LB 32896
**Cuphea carthagenensis* (Jack.) J.F. Macbr., LB 18618
Rotala ramosior (L.) Koehne, LB 33112 (P)

Magnoliaceae
Magnolia grandiflora L., LB 32545
Magnolia virginiana L., LB 26112 (P), 18777; LBJL 32963

Malvaceae
Hibiscus moscheutos L. subsp. *lasiocarpos* (Cav.) O.J. Blanchard, LB 33107
Malvastrum coromandelanum (L.) Garcke, LB 32947
Malvaviscus arboreus Cav. var. *drummondii* (Torr. & A. Gray) Schery, LB 33145; LBJL 32971
Modiola caroliniana (L.) G. Don, LBSH 33324
!*Sida lindheimeri* Engelm. & A. Gray, LB 32569
Sida rhombifolia L., LB 32641
Sida spinosa L., LB 32910 (P)

Marsileaceae
!*Marsilea vestita* Hook. & Grev. subsp. *vestita*, GW 3155

Melastomataceae
Rhexia mariana L. var. *mariana*, LB 32669

Melanthiaceae
!*Stenanthium gramineum* (Ker-Gawl.) Morong, GW 3500; LBSH 33510

Menispermaceae
Cocculus carolinus (L.) DC., LB 32835

Menyanthaceae
!*Nymphoides aquatica* (J.G. Gmel.) Kuntze, LB 25517 (P)

Molluginaceae
**Mollugo verticillata* L., LB 32901

Moraceae
Morus rubra L., LB 32525

Myricaceae
Morella caroliniensis (Mill.) Small, LB 26124 (P), 19774, 33161 (P); GW 3310

Morella cerifera (L.) Small, LB 28247(P)

Nymphaeaceae
Nuphar advena (Aiton) W.T. Aiton, GW 3289; LBSH 33251 (P)

Oleaceae
Chionanthus virginicus L., LB 18503, 20593, 33176 (P); LBJL 32976
Forestiera acuminata (Michx.) Poir., LB 32843; LBJL 32981 (P); MM 8225
Fraxinus americana L., LB 29431, 32502, 18590
Fraxinus pennsylvanica Marshall, LB 32711(P)
**Ligustrum sinense* Lour., LB 32652

Onagraceae
Ludwigia alternifolia L. LB 26120a (P), 18589, 18728, 32658
Ludwigia decurrens Walter, LB 18730, 32900
Ludwigia glandulosa Walter var. *glandulosa*, LB 32716
Ludwigia hirtella Raf., LB 18739b
Ludwigia leptocarpa (Nutt.) Hara, LB 33121 (P)
Ludwigia microcarpa Michx., LB 26120 (P), 25518 (P)
Ludwigia octovalvis (Jacq.) P.H. Raven, LB 18101(P), 32848
Ludwigia palustris (L.) Elliott, LB 25182, 33116 (P)
Oenothera biennis L., LB 32649; LBSH 33250 (P)
Oenothera laciniata Hill, LB 27717 (P), 20169 (P)
Oenothera speciosa Nutt., LBSH 33406

Ophioglossaceae
Botrychium biternatum Underwood, LB 18744, 33123 (P)
!*Ophioglossum vulgatum* L., GW 3193

Orchidaceae
!*Habenaria repens* Nutt., LB 5825 (P); JS 280 (P)
Platanthera clavellata (Michx.) Luer, LB 20591; LBJL s.n.
Platanthera cristata (Michx.) Lindl., LB 15431 (P); JL s.n. (P)
Spiranthes cernua (L.) Rich., LB 18861, 33137
!*Spiranthes ovalis* Lindl., LBJL 32959
Spiranthes praecox (Walter) S. Watson, GW 3257, 3380; LBSH 33367
Tipularia discolor (Pursh) Nutt., LB 18492, 18514, 18731; JL s.n.

Orobanchaceae
Epifagus virginiana (L.) W.P.C. Barton, LB 18163; LBSH 33329

Osmundaceae
Osmunda cinnamomea L., LB 18747
Osmunda regalis L. var. *spectabilis* (Willd.) A. Gray, LB 18579

Oxalidaceae
Oxalis corniculata L. var. *wrightii* (A. Gray) B.L. Turner, LB32654a, 33117 (P), 27715 (P); LBSH 33319
**Oxalis debilis* Kunth var. *corymbosa* (DC.) Lourteig, LBSH 33258 (P)
Oxalis lyonii Pursh, LBSH 33235
Oxalis violacea L., LB 32742

Passifloraceae
Passiflora incarnata L., LB 32657, 32662
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Phytolaccaceae
Phytolacca americana L., LBSH 33366

Pinaceae
Pinus echinata Mill., LBSM 33546
Pinus taeda L., LB 32630

Plantaginaceae
Plantago aristata Michx., LBSM 33536
**Plantago major* L., LBSH 33367
Plantago rhodosperma Dcne., LBSH 33384
Plantago virginica L., LBSH 33393

Platanaceae
Platanus occidentalis L., LB 32894

Poaceae
Agrostis hyemalis (Walter) Britton, Sterns & Poggenb., LBSH 33390
Agrostis perennans (Walter) Tuck. var. *perennans*, LB 18167, 33143, 33156 (P); LBJL 32956
Andropogon gerardii Vitman, GW 3210
Andropogon glomeratus (Walter) Britton, Sterns & Poggenb., LB 33160 (P)
Andropogon gyrans Ashe var. *gyrans*, GW 3209
Aristida oligantha Michx., GW 3212
Arundinaria gigantea (Walter) Muhl., LB 32539
Axonopus fissifolius (Raddi) Kuhlm, LB 32666
Axonopus furcatus (Flüggé) Hitchc., LB 32943
**Briza minor* L., LBSH 33379
**Bromus catharticus* Vahl, LBSH 33393
**Bromus japonicus* Thunb. ex Murray, LBSH 33380; LBSM 33550
!*Bromus pubescens* Muhl. ex Willd., LBSH 33453 (P)
!**Bromus secalinus* L., LBSM 33545
Cenchrus spinifex Cav., LB 32949
Chasmanthium latifolium (Michx.) H.O. Yates, LB 26107 (P), 18596, 32513
Chasmanthium laxum (L.) H.O. Yates, GW 2314; LBDB 33663
Chasmanthium sessiliflorum (Poir.) H.O. Yates, LB 32514, 32885
**Cynodon dactylon* (L.) Person, LB 32715 (P)
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark var. *acuminatum*, LBSH 33459 (P)
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark var. *lindheimeri* (Nash) Gould & C.A. Clark, LB 33093; LBSM 33528 (P), 33519
Dichanthelium boscii (Poir.) Gould & C.A. Clark, LB 29430, 29424, 29425; LBSH 33401 (H)
Dichanthelium commutatum (Schult.) Gould subsp. *commutatum*, LB 27742a (P), 18498
Dichanthelium dichotomum (L.) Gould subsp. *dichotomum*, LB 18602, 22562
Dichanthelium dichotomum (L.) Gould subsp. *microcarpon* (Muhl. ex Elliott) Freckmann & Lelong, LB 32818; LBJL 19177; LBSH 33371, 33435a (P)
Dichanthelium laxiflorum (Lam.) Gould, LB 27744 (P), 18504, LB 32661,18581
Dichanthelium oligosanthes (Schult.) Gould var. *oligosanthes*, LB 32824a; LBSM 33549
Dichanthelium oligosanthes (Schult.) Gould var. *scribnerianum* (Nash) Gould, LB 18521; LBJL 32965; LBSH 33314, 33454 (P)
Dichanthelium scoparium (Lam.) Gould, LBJL 32965
Dichanthelium tenue (Muhl.) Freckman & Lelong, LBSH 33435 (P)

Digitaria ciliaris (Retz.) Koeler, LB 32529a, 32645, 33092
**Digitaria ischaemum* (Schreb.) Muhl., LB 32747a
!*Echinochloa crus-pavonis* (Humb., Bonpl. & Kunth) Schult. var. *macer* (Wiegand) Gould, LB 32944
Echinochloa walteri (Pursh) Heller, LB 32911 (P), 33095
**Eleusine indica* (L.) Gaertn., LB 32631, 32530
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!*Eragrostis reptans* (Michx.) Nees, LB 18834, 32903, 33119 (P)
Eragrostis spectabilis (Pursh) Steud., LB 32942
Eustachys petraea (Sw.) Desv., LBSH 33453 (P)
Hordeum pusillum Nutt., LBSH 33382
Leersia lenticularis Michx., LB 32833
Leersia virginica Willd., LB 32690
!*Leptochloa panicea* (Retz.) Ohwi subsp. *mucronata* (Michx.) Nowack, LB 33100
!*Limnodea arkansana* (Nutt.) L.H. Dewey, LBSH 33394
**Lolium perenne* L., LB 33231a
Melica mutica Walter, LB 18482; LBSH 33218
!*Muhlenbergia schreberi* J.F. Gmel., LB 33170 (P)
Oplismenus hirtellus (L.) P. Beauv. subsp. *setarius* (Lam.) Mez, LB 32626
Panicum anceps Michx., LB 18706, 32862
Panicum brachyanthum Steud., LB 32925
Panicum dichotomiflorum Michx., LB 32895
Panicum gymnocarpon Elliott, LB 32834
**Panicum repens* L., LB 32642
Panicum rigidulum Bosc. ex Nees, LB 26106 (P), 33139
Panicum verrucosum Muhl., LB 18849
Panicum virgatum L., LB 33086
Paspalum laeve Michx., LB 32674
Paspalum langei (Fourn.) Nash, LB 32529
**Paspalum notatum* Flüggé, LB 32670
Paspalum plicatulum Michx., LBSH 33445 (P), 33513
Paspalum repens P.J. Bergius, LB 18824, 17512 (P), 32909 (P); LBJL 32984
Paspalum setaceum Michx., LB 32670a
**Paspalum urvillei* Steud., LB 32702; LBSM 33527 (P)
Phalaris angusta Trin., LBSH 33409
Phalaris caroliniana Walter, LBSH 33418
Piptochaetium avenaceum (L.) Parodi, LB 27720 (P), 18486; LBSH 33318
**Poa annua* L., LBSH 33207
Poa autumnalis Muhl. ex Elliott, LB 27742 (P), 18533; LBSH 33331
Saccharum baldwinii Spreng., LB 32921
Saccharum giganteum (Walter) Pers., LB 18858
+**Schedonorus arundinaceus* (Schreb.) Dumort., LBSH 33383
Schizachyrium scoparium (Michx.) Nash var. *divergens* (Hack.) Gould, GW 3208
!*Schizachyrium scoparium* (Michx.) Nash var. *scoparium*, LB 32917
!*Setaria corrugata* (Elliott) Schult., LB 28807
!+*Sphenopholis longiflora* (Vasey ex L.H. Dewey) Hitchc., LB 18542, 32263; LBSM 33522
+*Sphenopholis obtusata* (Michx.) Scribn., LB 18526; LBSH 33470
Sporobolus indicus (L.) R. Br., LB 32672
Steinchisma hians (Elliott) Nash, LBSM 33520
Tridens flavus (L.) Hitchc. var. *flavus*, LB 32665
Tridens strictus (Nutt.) Nash, LB 32915
Vulpia octoflora (Walter) Rydb., LB 18519; LBSH 33446 (P)

Polemoniaceae
Phlox pilosa L., LBSH 33326

Polygalaceae
Polygala polygama L., LBSH 33439 (P)

Polygonaceae
Brunnichia ovata (Walter) Shinners, LB 32507
Polygonum densiflorum Meisn., LB 32841
Polygonum hydropiperoides Michx., LB 32828a; LBSH 33421
Polygonum punctatum Elliott, GW 3288a; LB 32692, 32828
Polygonum virginianum L., LB 32522
**Rumex crispus* L., LBSH 33397
Rumex hastatulus Baldw., LBSH 33315

Polypodiaceae
Pleopeltis polypodioides (L.) E.B. Andrews & Windham var. *michauxianum* (Weath.) E.B. Andrews & Windham, LB 32510, 32961

Portulacaceae
!*Claytonia virginica* L., LBSH 33216

Potamogetonaceae
Potamogeton diversifolius Raf., LBSH 23353 (P)

Primulaceae
**Anagallis arvensis* L., LBSH 33232a
Anagallis minima (L.) Krause, LB 32680
Lysimachia radicans Hook., WRC 11354; LB 28170, 18682, 18170

Ranunculaceae
Clematis crispa L., GW 3303; LB 32512; 18862 (P); MM 8224
Clematis reticulata Walter, LB 32749
Ranunculus hispidus Michx. var. *nitidus* (Chapm.) T. Duncan, LB 27741a (P); LBSH 33225, 33220
**Ranunculus parviflorus* L., LB 18536
Ranunculus pusillus Poir., LB 18496
!*Thalictrum dasycarpum* Fisch. & Ave-Lall., GW 3231; LBSH 33232

Rhamnaceae
Berchemia scandens (Hill) K. Koch, LB 32914 (P)
Frangula caroliniana (Walter) A. Gray, LB 18513

Rosaceae
Crataegus brachyacantha Sarg. & Engelm., LB 32816; LBSH 33233
Crataegus marshallii Egglston, LB 32833
Crataegus spathulata Michx., GW 3216; LB 32511
Crataegus viridis L., GW 3298; LB 32712 (P), 32857
**Duchesnea indica* (Andrews) Focke, LB 33169 (P); LBSH 33255
!*Geum canadense* Jacq. var. *camporum* (Rydb.) Fernald & Weath., LB 32527, 18543; LBSH 33424
!*Prunus angustifolia* Marshall, LB 18685
Prunus caroliniana (Mill.) Aiton, LB 32926
!*Prunus mexicana* S. Watson, LBPR 33349

Prunus serotina Ehrhart, LB 32651
Prunus umbellata Elliott, GW 3328, 3334
Rubus argutus Link, LB 32622; LBSH 33234

Rubiaceae
Cephalanthus occidentalis L., LB 18490
Diodia teres Walter, LB 32746
**Galium aparine* L. GW 3221,N19
Galium obtusum Bigelow var. *obtusum*, LBSH 33410
Galium pilosum Aiton, LB 3257; LBSH 33469; LBSM 33533
Galium tinctorium (L.) Scop., GW 3202,3220, 3286; LBSM 33526 (P)
Houstonia pusilla Schoepf., LBSH 33206
Mitchella repens L., LB 32546, 18493, 29421
!+**Mitracarpus hirtus* DC., LB 18847, 32644
Oldenlandia boscii (DC.) Chapm., LB 18168, 22570
Oldenlandia uniflora L., LB 18171, 22569
**Sherardia arvensis* L., LBSH 33228
!*Spermacoce glabra* Michx., LB 17511 (P), 33096

Rutaceae
Ptelea trifoliata L var. *mollis* Torr. & A. Gray, LB 22571, 18479, 32931; LBSH 33375
Zanthoxylum calva-herculis L., LB 28254 (P)

Salicaceae
!*Populus deltoides* Bart. ex Marshall subsp. *deltoides*, LB 32518; GW 3232
Salix nigra Marshall, LBDB 33656

Sapindaceae
!*Cardiospermum halicacabum* L., LB 32839, 32905 (P)

Sapotaceae
Sideroxylon lanuginosum Michx., GW 3268; LBPR 33346

Saururaceae
Saururus cernuus L., LB 18577; LBSH 33437 (P)

Scrophulariaceae
Agalinis fasciculata (Elliott) Raf., LB 32871
Agalinis purpurea (L.) Penn., LB 33135
Aureolaria grandiflora (Benth.) Penn., LB 26109 (P)
Gratiola brevifolia Raf., LB 18619
Gratiola neglecta Torr., LB 18538
Gratiola pilosa Michx., LB 18617
Gratiola virginiana L., LB 27726 (P), 18500; LBSH 33402 (H)
Leucospora multifida (Michx.) Nutt., LB 18834
Lindernia dubia (L.) Penn., LB 18830, LB 33118 (P)
!**Mazus pumilus* (Burm.f.) Steenis, LBSH 33227a
Mecardonia acuminata (Walter) Small, WRC 11351; LB 33148
Mecardonia procumbens (Mill.) Small, GW 3233
Micranthemum umbrosum (J.F. Gmel.) S.F. Blake, LB 18852a, 33166 (P)
Mimulus alatus Aiton, LB 18737, 5838 (P); LBJL 32973
Nuttallanthus texana (Scheele) Sutton, LBSH 33320
!*Pedicularis canadensis* L., LBSH 33322
!+*Penstemon tenuis* Small, LB 18535; LBPR 33348; LBSH 33422
Scoparia dulcis L., LB 18732, 32941
**Veronica arvensis* L., LBSH 33203, 33239
Veronica peregrina L. subsp. *xalapensis* (Kunth) Pennell, GW 3314, 3366
!**Veronica persica* Poir., LBSH 33229

Selaginellaceae
Selaginella apoda (L.) Spreng., LB 27738 (P), 20168 (P)

Smilacaceae
Smilax bona-nox L., LB 32627
Smilax glauca Walter, LB 18584, 32753
Smilax laurifolia L., LB 27736, 18781, 18746
Smilax pumila Walter, LB 18599; LBJL 32967
Smilax rotundifolia L., LB 33175 (P)
Smilax smallii Morong, LB 32639

Solanaceae
!*Physalis angulata* L., LB 18841, 33120 (P)
Physalis heterophylla Nees, LB 25168, 32886; LBSH 33238; LBPR 33345
Solanum carolinense L., LB 33144

Sparganiaceae
Sparganium americanum Nutt., LB 15436 (P), 33171 (P), 25516a

Sphenocleaceae
!**Sphenoclea zeylandica* Gaertn., LB 18822

Styracaceae
Styrax americana Lam., LBJL 32980 (P), 33164 (P), 33141; LB 18165

Symplocaceae
Symplocos tinctoria (L.) L. Her., LB 32535, 18508

Thelypteridaceae
Thelypteris kunthii (Desv.) Morton, LB 32557a, 28244 (P)

Tiliaceae
Tilia americana (L.) var. *caroliniana* (Mill.) Castig, LB 32531

Typhaceae
Typha latifolia L., LBSH 33441 (P)

Ulmaceae
Celtis laevigata Willd., LB 32891
Planera aquatica L., LB 18819 (P), LB 32748, 27745 (P)
Ulmus alata Michx., LB 32655
Ulmus americana L., LB 32912 (P)
!*Ulmus crassifolia* Nutt., LB 32709 (P)

Urticaceae
Boehmeria cylindrica (L.) Sw., LB 26105, 32889
!*Urtica chamaedryoides* Pursh, LB 25180; GW 3156; LBSH 33243

Valerianaceae
Valerianella radiata (L.) Dufr., LB 18475; LBSH 33237

Verbenaceae
Callicarpa americana L., LB 32623
**Glandularia pulchella* (Sweet) Tronc., LBSH 33234a
**Verbena brasiliensis* Vell., LB 32701
Verbena halei Small, LBSH 33385
**Verbena rigida* (L.) Spreng., LBSH 33442 (P)

Violaceae
Viola lanceolata L., LB 27721(P)
Viola palmata L., GW 3192, 3306, 3307; LBSH 33214
Viola primulifolia L., LB 27731(P), 27716, 18495, 33167 (P)
Viola sororia Willd. var. *missouriensis* (Greene) McKinney, GW 3218, 3302; LBSH 33226
!*Viola sororia* Willd. var. *sororia*, LBDB 33659

Vitaceae
Ampelopsis arborea (L.) Koehne, LB 32658
!*Ampelopsis cordata* Michx., LB 32515, 32658; LBPR 33342; GW 3246
Parthenocissus quinquefolia (L.) Planch., LB 32521
Vitis aestivalis Michx., LB 32660
Vitis cinerea (Engelm.) Engelm. ex Millardet var. *cinerea*, GW 3269
!*Vitis mustangensis* Buckley, LBDB 33654a
Vitis palmata Vahl, LB 18820a (P); GW 3244
Vitis rotundifolia Michx., LB 32635

Xyridaceae
Xyris jupicai L. Rich., LB 26121, 26116 (P), 32668

NOTES

Eupatorium semiserratum. See Brown et al. (2007) regarding the status of this species in Texas.

Prenanthes barbata. Poole et al. (2007) mapped it in 12 Texas counties. This is the first record for Liberty County.

Verbesina helianthoides. See Brown et al. (2007) regarding this species in Liberty County.

Silene subciliata. Poole et al. (2007) mapped it in 8 Texas counties. All known Liberty County records are from the Menard Creek Unit.

Carex typhina. Both Stanley Jones in Diggs et al. (2006) and Turner et al. (2003) mapped it in 7 northeast Texas counties. However, in Diggs et al. (loc. cit.) there is one record farther south in Jasper County. Our collection is a new county record farther south then those previously recorded. There were numerous individuals on sandy alluvial soil along Menard Creek a short distance upstream from the confluence with the Trinity River.

Schedonorus arundinaceus. We are following Darbyshire (2007). Other synonyms are *Festuca arundinacea* Schreb. and *Lolium arundinaceum* (Schreb.) Darbysh.

Sphenopholis longiflora. Both this grass and *S. obtusata* are present in this unit. In many publications, *S. longiflora* is treated as a variety of *S. obtusata*. At least in this unit, species rank is justified for various reasons including no plants were found with intermediate morphology; habitat difference, with *S. longiflora* in bottomland habitats and *S. obtusata* in upland habitats; and anthesis period, with *S. longiflora* in flower in March and shedding mature spikelets when *S. obtusata* is coming into flower in April.

Penstemon tenuis. Some authors merge this species with *P. laxiflorus*. All of our plants had glabrous stems or sparse hairs in thin lines, the flowers were pink, and were collected in bottomland hardwoods; thus are referable to this species. We found no penstemons that we could call *P. laxiflorus*. The differences between the 2 species are readily discernable when both are observed in the field.

Mitracarpus hirtus. See Brown et al. (2007) regarding the presence of this species in east Texas.

DISCUSSION

There are 127 families and 396 genera for the 689 taxa (619 native) on the Menard Creek Corridor Unit list. Eight families: Asteraceae (88 taxa), Poaceae (82 taxa), Cyperaceae (67 taxa), Fabaceae (51 taxa), Scrophulariaceae (21 taxa), Lamiaceae (18 taxa), Euphorbiaceae (16 taxa), and Fagaceae (13 taxa) account for 51% of all taxa collected. The genera with 10 or more taxa are *Carex* (35 taxa), *Cyperus* (12 taxa), *Quercus* (11 taxa), *Dichanthelium* (11 taxa), and *Juncus* (10 taxa).

While it is the case that our list is incomplete, as are all floras, we believe that we have collected 90+ % of the taxa. We estimate that the Menard Creek Corridor Unit has about 625 to 650 native species/taxa.

Of the 7 Units inventoried so far, this unit has 86 taxa that have not been found in the other surveyed units including a preliminary checklist of the Jack Gore Baygall/Neches Bottom Unit. Thus 12% of the Menard Creek Unit taxa have not been found in the other inventoried units.

ACKNOWLEDGMENTS

This study was supported in part by an All Taxa Biological Inventory grant (ATBI) from the Big Thicket Association of Saratoga, Texas. We thank Ray C. Telfair II and Barney Lipscomb who carefully read the paper and pointed out a number of errors that hopefully we were able to correct.

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BOOK NOTICE

Flora of China Editorial Committee. 2008 (December). **Flora of China, Vol. 7. Menispermaceae through Capparaceae.** (ISBN Vol. 7: 978-1-930723-81-8, hbk.). Science Press (Beijing) and Missouri Botanical Garden Press (St. Louis), P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. (**Orders:** www.mbgpress.org, mbgpress@mobot.org, 1-877-271-1930). $125.00, 499 pp., 8 3/4" x 11 1/4".

From the publishers.—"Eleven plant families are described in this volume. Among these, the Capparaceae include the caper (*Capparis spinosa*); the Lauraceae include the main source of camphor (*Cinnamomum camphora*), the spices cassia (*C. cassia*) and cinnamon (*C. verum*), and the cultivated bay laurel (*Laurus nobilis*); the Magnoliaceae include the Asian tulip tree (*Liriodendron chinense*), found only in China and Vietnam, and some 110 species of magnolias that are treated either in 12 separate genera or all in *Magnolia*; the Myristicaceae include the source of nutmeg and mace (*Myristica fragrans*); and the Papaveracee include the horticulturally important poppies, *Meconopsis* and *Papaver*, as well as the very diverse genus *Corydalis*, which has 357 species in China."

Editors Wu Zhengyi, Peter H. Raven, and Hong Deyuan state, "[This] is the 16th of the 24 text volumes in the series. It includes 11 families, 95 genera, and 1226 species, among which four genera and 778 species (64%) are endemic to China, and eight genera and 16 species (1.3%) are introduced to China." The families covered are (in alphabetical order): Calycanthaceae, Capparaceae, Cleomaceae, Hernandiaceae, Illiciaceae, Lauraceae, Magnoliaceae, Menispermaceae, Myristicaceae, Papaveraceae, and Schisandraceae. Also included in the text: Preface, Introduction, Acknowledgments, List of Nomenclatural Novelties Published in this Volume of the *Flora of China*, Index to Chinese Names, Index to Pinyin Names, Index to Scientific Names, Index to Families in the *Flora of China* and the *Flora Reipublicae Popularis Sinicae*, and Published Volumes of the *Flora of China* and the *Flora of China Illustrations*. A large map of China and its 35 Administrative Divisions is printed on both the inside front cover/front endpaper and the inside back cover/back endpaper.

J. Bot. Res. Inst. Texas 3(1): 456. 2009

CYPERUS PILOSUS (CYPERACEAE) NEW TO THE FLORA OF TEXAS

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ABSTRACT

Cyperus pilosus is reported new to Texas and a dichotomous key is presented to distinguish it from congeners in that state.

RESUMEN

Cyperus pilosus se cita nuevo para Texas y se presenta una clave dicotómica para diferenciarlo de sus congéneres en el estado.

Cyperus pilosus Vahl is widely distributed in tropical or subtropical areas of the Old World (Kükenthal 1935–1936). It is a common weed of rice in Asia (McGivney 1938; Bryson & Carter 2008) and is known from Hawaii based upon a single historical collection made in 1916 (Wagner et al. 1999). *Cyperus pilosus* was first reported in the continental United States from Louisiana, where it was apparently introduced from Asia as a contaminant of rice seed (O'Neill 1938). Subsequently, it has been reported from Florida (Burkhalter 1985), Mississippi (Bryson & Carter 1992), South Carolina (Tucker et al. 2002), and Georgia (Carter et al. 2009). *Cyperus pilosus* inhabits hydric soils of wet ditches, rice fields, edges of ponds, and wetlands. It has not previously been reported from Texas (Jones et al. 1997; Tucker et al. 2002; Diggs et al. 2006), and the nearest mapped locality is in nearby Calcasieu Parish, Louisiana (Thomas & Allen 1993).

The specific epithet *pilosus* is descriptive of the hispidulous rachis. The species is illustrated in Figure 1. If inserted in the key to *Cyperus* immediately after the first lead of couplet 8 on page 1133 in Diggs et al. (2006), the following couplet will enable the identification of *C. pilosus* in eastern Texas.

8. Plant with elongated slender rhizomes; culm sharply triquetrous, easily compressed ____________ **C. pilosus**
8. Plant cespitose, without elongated rhizomes; culm subterete to obtusely trigonous, not easily compressed ____________ **continue with couplet 9**

Voucher specimens: **TEXAS. Newton Co.:** Caney Creek Park, S of Hwy. US 190 in Newton, 30° 50' 842"N 93° 45' 802"W, 30 Oct 2008, *Allen and Lewis 21096* (VSC), *Allen and Lewis 21098* (BRIT, FTPK, VSC).

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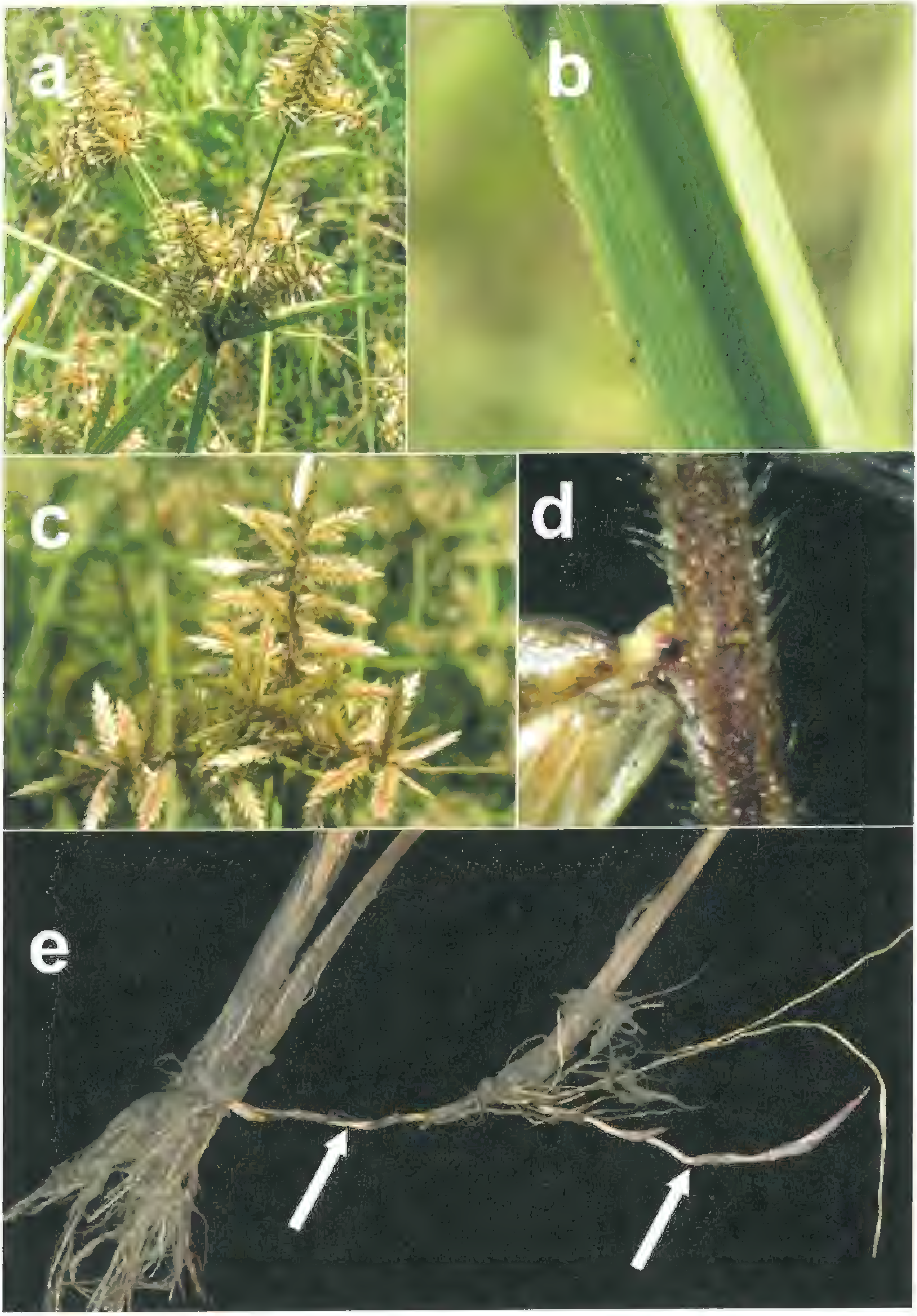

Fig. 1. *Cyperus pilosus*. **1a.** Inflorescence habit. **1b.** Detail of triquetrous culm showing antrorse prickle hairs on wing-edges. **1c.** Inflorescence ray with spikelets. **1d.** Hispidulous rachis. **1e.** Rhizomes (arrows) and connected bases of culms. Photographs from *R. Carter 16081*, Bacon County, Georgia.

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BOOK NOTICE

FLORA OF CHINA EDITORIAL COMMITTEE. 2008. **Flora of China Illustrations, Vol. 12. Hippocastanaceae through Theaceae.** (ISBN Vol. 12 illustrations: 978-1-930723-79-5, hbk.). Science Press (Beijing) and Missouri Botanical Garden Press (St. Louis), P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. (**Orders:** www.mbgpress.org, mbgpress@mobot.org, 1-877-271-1930). $125.00, 475 pp., 8 3/4" × 11 1/4".

From the publishers.—"Volume 12 of the illustrations series is devoted to 18 plant families, several of which have economic and horticultural importance: Actinidiaceae, source of the kiwi fruit; Balsaminaceae, with the colorful *Impatiens* genus; Malvaceae, with *Gossypium*, the genus that provides cotton, and the mallows and hollyhocks; Theaceae, including the tea plant *Camellia sinensis*, as well as the ornamental camellias; and Vitaceae, notable for *Vitis vinifera*, the grapevine."

Editors Wu Zhengyi, Peter H. Raven, and Hong Deyuan state, "This publication is the 13th in a series of 24 volumes of *Flora of China Illustrations*. It accompanies *Flora of China* (FOC) Volume 12, which was published in 2007 and treated 125 genera with 1275 species in 18 families. This volume of illustrations includes 450 plates representing a total of 937 species, 14 subspecies, and 202 varieties in 123 genera in 18 families." Also included in the text: Preface, Acknowledgments, Index to Chinese Names, Index to Pinyin Names, Index to Scientific Names, Index to Families in the *Flora of China* and the *Flora Reipublicae Popularis Sinicae,* and Published Volumes of the *Flora of China* and the *Flora of China Illustrations*. A large map of China and its 35 Administrative Divisions is printed on both the inside front cover/front endpaper and the inside back cover/back endpaper.

CRYPTOSTEGIA GRANDIFLORA (APOCYNACEAE: ASCLEPIADOIDEAE), A NEW NON-NATIVE WEED FOR TEXAS

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ABSTRACT

Cryptostegia grandiflora is naturalized in Starr County, Texas, where it has been observed at two localities along the Rio Grande. It is abundant at both sites and often densely covers entire trees.

RESUMEN

Cryptostegia grandiflora está naturalizada en el condado de Starr, Texas, donde ha sido observada en dos localidades a lo largo del Río Grande. Es abundante en ambos lugares y a menudo cubre densamente árboles enteros.

Cryptostegia grandiflora (Roxb. ex R. Br.) R. Br. (Apocynaceae, Asclepiadoideae; Palay rubbervine) has been discovered growing outside of cultivation in several places in Starr Co., Texas. It has not been previously reported or unequivocally confirmed as a naturalized member of the Texas flora (Nesom 2009).

TEXAS. Starr Co.: Roma, riparian vegetation along Rio Grande below Observation Deck of Roma Bluffs World Birding Center, completely and densely enshrouding ebanos (*Ebenopsis ebano*) up to 10 m high, fruiting, 17 Jan 2009, *T.F. Patterson 2009-1 with E.C. Patterson* (BRIT, TEX); Rio Grande City, riparian forest along the Rio Grande below Ft. Ringgold, fruiting, 17 Jan 2009, *T.F. Patterson 2009-2 with E.C. Patterson* (BRIT, TEX). ***Cryptostegia grandiflora*** was much earlier collected in south Texas, but it is not clear that this plant was growing outside of cultivation: **Cameron Co.:** Brownsville, sandy soil, alt. 30 ft, scandent shrub, 20 Oct 1923, *Runyon 566* (TEX).

At the Roma Bluffs, *Cryptostegia grandiflora* densely covers 13 trees of popinac (*Leucaena leucocephala*), Berlandier ash (*Fraxinus berlandieriana*), and ebano (*Ebenopsis ebano*). Over an area of ca. 1 acre, growing from the banks of the Rio Grande up the slope to the backyards of houses lining the bluff. This Roma neighborhood may have been the source of the escaped Palay rubbervine.

The Ft. Ringgold site occurs ca. 22 miles downriver from the Roma Bluffs in a riparian forest far away from any houses in Rio Grande City. *Cryptostegia grandiflora* densely covers over 60 trees of salt cedar (*Tamarix aphylla*) and sugar hackberry (*Celtis laevigata*), spread over ca. 3 acres. Most of the rubbervine drapes salt cedars that occur on the first terrace above the river. The species also covers hackberries mostly in the riparian forest at the level of the river inland from the *Phragmites*-covered bank. Many of the most densely covered hackberries have died. Both areas are periodically flooded by the Rio Grande and it may have been during these floods that logs with attached *C. grandiflora* and the copious wind- and water-dispersed seeds transported the rubbervine downriver to Ft. Ringgold.

Cryptostegia grandiflora is native to Madagascar, where it occurs in riverine and seasonally flooded forests in the dry, southwest part of the country, and it is widely adventive in other parts of the world. It is reported to be invasive in the United States in the Florida Keys, Monroe Co. (Wunderlin & Hansen 2003, 2008) and it also is naturalized in Mexico, the West Indies, Australia, and Pacific Islands (PIER 2007). Standley (1924) reported that *C. grandiflora* was thoroughly naturalized in Sinaloa, and a "distributed query" to major herbaria with Mexican specimens (REMIB 2008) shows subsequent collections from Baja California Sur, Guerrero, Jalisco, Michoacan, Nayarit, Puebla, Sinaloa, Sonora, Tamaulipas, and Yucatán.

The genus *Cryptostegia* includes only two species, *C. grandiflora* and *C. madagascariensis* Bojer ex Decne. (Marohasy & Forster 1991), both endemic to Madagascar and both widely cultivated as ornamentals. Both species are naturalized and invasive in Florida and in Australia. In Hawaii, "Both species are usually identified

as *C. grandiflora* R. Br., but nearly all Hawaiian cultivated plants proved on careful inspection to be *C. madagascariensis*" (Staples et al. 2006). Apparently all or most reports for the Pacific area have been re-identified as *C. madagascariensis* in the Pacific Island Ecosystems at Risk account (PIER 2007) and previous reports of naturalized *C. grandiflora* should be evaluated in light of the possibility of confusion with its closely similar congener. Descriptions of both species are given on the pages in the PIER online database, and color photos of both also are available (PIER 2007; HEAR 2008). The following key, based on the work of Marohasy and Forster (1991), can be used to distinguish the species:

1. Stems with prominent, few lenticels; leaf blades with 14–16 pairs of secondary veins; corollas 3–4 cm long; corona filaments entire; follicles 5.8–9.9 cm long ____ **Cryptostegia madagascariensis**
1. Stems with small, numerous lenticels; leaf blades with 11–13 pairs of secondary veins; corollas 5–6 mm long; corona filaments bilobed; follicles 10–15.4 cm long ____ **Cryptostegia grandiflora**

Diagnostic features of *Cryptostegia grandiflora*: Climbing, lactiferous subshrubs; leaves opposite, simple, thick, evergreen, glabrous, blades broadly oblong to elliptic, 4–10 cm x 3–5 cm, apices abruptly acuminate; flowers 6–12 in terminal cymes, corollas reddish purple to pale pink, tubes campanulate, 2–4.5 cm long, lobes spreading, 2–4 cm long; follicles fusiform-ovoid, 10–15.4 cm long. "Large *C. grandiflora* can produce more than 8000 wind dispersed seeds in a single reproductive episode and can set seed at least twice per year. More than 90% of seeds will germinate within 10 days of moisture becoming available. Few, if any, seeds survive for more than 12 months in the soil" (Grice 1996).

In Australia, *Cryptostegia grandiflora* is "found in Queensland in the dry tropical areas often fringing streams and river systems including adjacent hills and pastures. It smothers vegetation replacing native species, particularly in areas degraded by stock. [It] Hinders pastoralism and reported to be toxic to livestock" (Smith 2002, p. 47). A remarkable photo shows a vast area in north Queensland, including ground, shrubs, and trees, completely covered by the viny growth (Invasive Species Council 2008), and accompanying notes describe the species as "arguably Australia's worst weed." A small area at the Ft. Ringgold riparian site appears similar to the Queensland photo with *C. grandiflora* completely covering trees, shrubs, and ground. The viny undergrowth is impenetrable. The spread of Palay rubbervine should be of concern to both ranchers and the Lower Rio Grande Valley National Wildlife Refuge with refuge tracts from Falcon Dam to the mouth of the Rio Grande. Pastures and refuge tracts along the Rio Grande should be monitored for the first arrival of rubbervine, so it can be eradicated before it becomes established.

There apparently are no restrictions on the sale of either species of *Cryptostegia* in the United States, and both are included on recent versions of the "Nursery eligible plant list and plant price schedule" for Texas, Oklahoma, and New Mexico (FCIC 2008). *Cryptostegia grandiflora* is offered for sale by nurseries in Florida and Texas and was offered for "swap" on a 2006 Texas gardening forum on the internet.

ACKNOWLEDGMENTS

We are grateful to David Lemke and Barney Lipscomb for their helpful review comments and to Elena Castelo Patterson for her help in the field.

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BOOK NOTICE

FLORA OF CHINA EDITORIAL COMMITTEE. 2008. **Flora of China Illustrations, Vol. 13. Clusiaceae through Araliaceae.** (ISBN Vol. 13 illustrations: 978-1-930723-80-1, hbk.). Science Press (Beijing) and Missouri Botanical Garden Press (St. Louis), P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. (**Orders:** www.mbgpress.org, mbgpress@mobot.org, 1-877-271-1930). $125.00, 491 pp., 8 3/4" x 11 1/4".

From the publishers.—"Volume 13 of the illustrations series is devoted to 33 plant families, a number of which are of horticultural or agricultural importance or are otherwise distinctive: Violaceae, with its white, purple, and yellow violets; Passifloraceae, the passion flower family; Caricaceae, of which the genus *Carica* furnishes us with the papaya fruit; Begoniaceae, with *Begonia*, noted for its ornamental flowers and foliage; Cactaceae, featuring the *Cactus* genus; Thymelaeaceae, including ornamental shrubs *Daphne* and *Edgeworthia* used for the manufacture of paper and medicines; Trapaceae, the water chestnuts; Nyssaceae, containing genus *Camptotheca*, source of the anticancer drug camptothecin, and *Davidia*, the dove tree, which naturally occurs only in China; Onagraceae, including evening primrose and *Epilobium* or willowherb; and Araliaceae, containing the ivies as well as *Panax* or ginseng."

Editors Wu Zhengyi, Peter H. Raven, and Hong Deyuan state, "This publication is the 14th in a series of 24 volumes of *Flora of China Illustrations*. It accompanies *Flora of China* (FOC) Volume 13, which was published in 2007 and treated 151 genera with 1288 species in 33 families. This volume of illustrations includes 470 plates representing a total of 774 species, 12 subspecies, and 18 varieties in 157 genera of 33 famillies." Also included in the text: Preface, Acknowledgments, Index to Chinese Names, Index to Pinyin Names, Index to Scientific Names, Index to Families in the *Flora of China* and the *Flora Reipublicae Popularis Sinicae,* and Published Volumes of the *Flora of China* and the *Flora of China Illustrations*. A large map of China and its 35 Administrative Divisions is printed on both the inside front cover/front endpaper and the inside back cover/back endpaper.

TOURNEFORTIA HIRSUTISSIMA (BORAGINACEAE) NEW TO THE FLORA OF TEXAS

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ABSTRACT

Tournefortia hirsutissima (Boraginaceae) is reported for extreme south Texas, a new record for the state of Texas.

RESUMEN

Tournefortia hirsutissima (Boraginaceae) se cita del extremo sur de Tejas, es el primer registro para el estado de Tejas.

Tournefortia hirsutissima L. (Chiggery Grapes, Mata de Nigua) is native to various parts of Mexico, Central and South America, and the West Indies (Standley1924). It also grows in Florida (Wunderlin & Hansen 2003) but has not been reported for Texas (Turner et al. 2003). It is a sprawling and climbing shrub reaching at least 5 meters in height (Fig. 1). The stems and leaves are covered with stiff hairs which can cause irritation to the skin. The leaves are alternate, the blades ovate to elliptic and up to 15 cm long. The flowers, in branching cymes, have a fragrance somewhat like that of orange blossoms. The corollas are white, actinomorphic, ca. 1 cm broad, the tubes 4–5 mm long. The fruit are white drupes ca. 8 mm broad, each with one small black dot where the style has fallen, and containing 2–4 mericarps (Fig. 2).

Tournefortia hirsutissima has been given many common names in different countries. Both of the two that we have listed refer to the belief that rubbing an infected area with a leaf will kill or remove chiggers. The Spanish name means "chigger killer."

The plant was called to our attention by Mary Ann and David Sato through a mutual friend, Mike Heep. It was growing on the Sato property along Hudson Street in San Benito, Cameron County, Texas. We visited their home in March and April of 2007. The liana was growing next to the road. It was very large, covering an estimated 7 meter square area and growing 5 meters into the trees. Three more individuals were growing at the back of the property. The Satos said that they had not planted them and that they grew without any care. We suspect that the plants arrived by natural means, probably as seeds deposited by birds. Llera and El Encino, two collection sites in Tamaulipas, Mexico, are less than 400 km from San Benito.

Since the plant we examined was so robust, flowering and fruiting freely, it seems that it will gradually spread to other areas, at least in years when rains are abundant. It appeared to be old enough to have survived some of our drier years, although its native habitat generally receives more rainfall than Cameron County. It probably would not be so lush during the dry times.

Voucher specimens: **TEXAS. Cameron Co.:** S of San Benito on Sam Houston, E on Hudson. One large sprawling liana, at roadside, occupying an area about 20' × 20', climbing 15' high into trees, 31 Mar 2007, *Richardson and King* 3315 (BRIT, TEX); S of San Benito on Sam Houston, E on Hudson, one large sprawling liana, at roadside, occupying an area about 20' × 20', climbing 15' high into trees, 9 Apr 2007, *Richardson and King* 3320 (BRIT, TEX).

ACKNOWLEDGMENTS

We thank Mary Ann and David Sato and their friend Mike Heep for noticing and bringing *Tournefortia hirsutissima* to our attention. Monique D. Reed and an anonymous reviewer provided helpful reviews.

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Fig. 1. *Tournefortia hirsutissima*. Flowers.

Fig. 2. *Tournefortia hirsutissima*. Fruit.

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The Delzie Demaree Travel Award was established in 1988 honoring **Delzie Demaree** who attended 35 out of a possible 36 symposia before he died in 1987. Delzie Demaree was a frontier botanist, explorer, discoverer, and teacher. His teaching career as a botanist began in Arkansas at Hendrix College in 1922. He also taught botany at the University of Arkansas, Navajo Indian School, Yale School of Forestry, Arkansas A&M, and Arkansas State University at Jonesboro where he retired as professor emeritus in 1953. One of the things he enjoyed most as a botanist was assisting students with their field botany research.

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ISSN 1934-5259